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New York Botanical Garden, Bronx Park, New York, N.Y.

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HELEN M. TRELEASE
Box 42, Schermerhorn Hall, Columbia University, New York, N.Y.

Editor
BERNARD O. DODGE, PH.D.

Bibliographer
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Tertiary pollen

I. Pollen of the living representatives of the Green River flora

R. P. Wodehouse

(with plates 20–22 and three text figures)

It is the common complaint among paleobotanists that is is impossible to identify the pollen found in Tertiary deposits because there are no adequate descriptions and keys to the living species. In order to overcome completely this disability it would be necessary to acquire a familiarity with the pollen-grain forms of nearly every living species of flowering plant, a task far too great to be encompassed within the span of a single life. The next best thing is to acquire a familiarity with the living representatives of the known fossil flora of the formations in question, and to supplement this with a knowledge of the pollen-grain forms of as many as possible of the wind pollinated species which might have contributed their pollen to the deposits and yet not have grown near enough to the places of deposition to be otherwise represented. These latter I shall treat at considerable length in my book[1] which is now in press. The present paper presents my studies on the pollen of the remaining living representatives of the Green River flora of which material was available, and it is hoped that it will further assist in the identification of at least some of the many species found in the Green River shales. I plan to make the pollen of the Green River formation the subject of the second paper of this series treating Tertiary pollen.

The enormous numbers of beautifully preserved pollen grains in the Green River shales have frequently been commented upon by investigators of that formation. As long ago as 1917, C. A. Davis recorded, in Winchester's paper on The Oil Shales of the U. S. A., the presence of *Picea* and *Pinus* pollen. Bradley (1929), in his discussion of the fresh water algae of the Green River formation of Colorado says: "Organic matter consists of complete or fragmentary organisms such as algae, fungi, protozoa, insects and parts of higher plants, as spores pollen grains or minute pieces of tissue," and again (1931): "Pollens in great numbers and diversity occur in the oil shale, and many of them show their structural characters with fair clarity. If these pollens could surely be referred to their proper genera they would shed much additional light upon the flora of the Green River epoch. Unfortunately the morphology of pollen grains is imperfectly known, and consequently they have never been accurately correlated with classified plants."

[1] Morphology of the pollen grains, Charles C Thomas, publisher.

The Bulletin for May (59: 241–312) was issued 24 May, 1932.

Unquestionably a greater knowledge of these pollen grains would correspondingly extend the known flora of the formation. For example Brown (1929) states: "The presence of conifers in this flora, hitherto indicated only by pollen grains in the oil shale, is now further established by the finding of what appears to be coniferous leaves and a winged seed." It so happens that pollen grains of the winged-grained Abietineae, such as *Picea* and *Pinus* are among the commonest in the shales, yet, as may be gathered from the above statement, the occurrence of other parts of the trees is relatively infrequent. This is probably because the Abietineae of that epoch were mostly upland species, not favorably situated for their preservation in the low-lying lakes and ponds in which the materials of the shales are believed to have been deposited; but the pollen, being buoyant and carried great distances by air currents, could well come to rest in such places even though the trees grew many miles distant. It is to be expected, therefore, that in the shales will be found the pollen of many species which had scarcely any chance of being otherwise preserved. Furthermore, many of the identified plant fragments of the Green River flora are of species which, judged by their modern representatives, must have shed in that epoch a great abundance of pollen well adapted to preservation. Finding the pollen of such species in the shales would serve as a valuable check on identification based on fossil leaves or other fragments. Conversely the absence of the pollen of these species might cast some doubt upon the correctness of identification based upon small or indefinite fragments of the plants.

The beauty and perfection of the preservation of such minute and delicate structures as pollen grains is a constant source of admiration and wonder. Some of the grains are as perfectly preserved in the material of the shales as if they had been imbedded in celloidin or balsam expressly for microscopic examination. Obviously the principal thing that is needed to render this beautiful record available is a more complete knowledge of the living representatives of that flora.

"The Green River is a Middle Eocene formation, about 2000 feet in thickness and of threefold character, comprising a lower group of light brown to buff sandy calcareous shale, and a middle group of darker shale, and an upper group of light colored sandy shale. The formation originally covered an area about 300 by 150 miles in the contiguous corners of Colorado, Utah and Wyoming, but erosion subsequent to the time when this area ceased to be a basin of lacustrine deposition and was elevated several thousand feet, has deeply dissected parts of it and has thereby isolated patches of the formation." (Brown, 1929.) One of these areas, the Piceance Creek basin, where the Green River formation is now exposed,

is about 95 miles long from north to south, and about 46 miles wide. Another, the Uinta Basin, where the formation is exposed, is a strip about 135 miles long from east to west and 46 miles wide at the widest place. There are two other areas of comparable extent, lying to the north of the Uinta Mountains in Wyoming, but these have been less fully studied. The location and distribution of these areas are shown in the maps of Bradley's paper (1931).

The flora of this ancient formation, as far as it is at present known, includes about 130 species. These are predominantly subtropical mesophytes, totally unlike the flora now occupying the region. According to Brown (1929) the presence of such forms as palms, *Planera* and *Acrosticum* which require an abundance of rain fall and a warm climate, together with such species as *Quercus*, *Populus*, *Betula* and *Liquidambar* "point to the conclusion that this flora grew in a warm temperate region, a part of which, at least, received a plentiful supply of rain." Such a climate is probably not duplicated in the world today but "the climatic conditions of the southeastern Gulf states plus that of parts of the Great Valley of California would . . . roughly approximate the Green River Lake Area." As will be seen from looking over the following lists, the species which are represented in the Green River flora belong predominantly to groups having their centers of concentration now in Mexico, Central America and the northern part of South America, as if the climatic changes which have taken place since the Green River epoch have been such as to force the ancient flora southward even as far as equatorial America. Whether this was the case, or the Green River flora was but a northward extension in Eocene times of a southern flora is still an open question.

The Green River Flora

A list of the families and genera compiled from Knowlton (1923) and Brown (1929)

Coniferales: *Taxites, Picea.*
Sparganiaceae: *Sparganium.*
Gramineae: *Arundo.*
Cyperaceae: *Cyperus, Cyperacites.*
Arecaceae: *Geonomites, Sabal, Flabellaria.*
Pontederiaceae: *Pontederia.*
Juncaceae: *Juncus.*
Nymphaeaceae (Cabombaceae): *Brasenia.*
Salicaceae: *Salix, Populus.*
Myricaceae: *Myrica, Comptonia.*
Juglandaceae: *Hicoria, Juglans.*
Betulaceae: *Betula.*
Fagaceae: *Quercus.*
Ulmaceae: *Planera, Celtis.*

MORACEAE: *Ficus.*
PROTEACEAE: *Lomatia, Banksia.*
LAURACEAE: *Oreodaphne, Pinelea.*
ROSACEAE: *Chrysobalanus, Amygdalus.*
CRASSULACEAE: *Sedum.*
LEGUMINOSAE: *Cassia, Dalbergia, Leguminosites, Sophora.*
MIMOSACEAE: *Mimosites.*
MALPIGHIACEAE: *Banisteria.*
SIMARUBACEAE: *Ailanthus.*
ANACARDIACEAE: *Rhus, Schmaltzia, Anacardites.*
CELASTRACEAE: *Celastrophyllum, Euonymus, Maytenus.*
SAPINDACEAE: *Thouinia, Sapindus.*
ACERACEAE: *Acer.*
AQUIFOLIACEAE: *Ilex.*
TILIACEAE: *Grewiopsis.*
RHAMNACEAE: *Zizyphus.*
VITACEAE: *Cissus. Parthenocissus.*
STERCULIACEAE: *Sterculia.*
TERNSTROEMIACEAE: *Ternstroemites.*
OLEACEAE: *Fraxinus.*
APOCYNACEAE: *Apocynophyllum, Apocynospermum.*
MYRTACEAE: *Eucalyptus.*
ARALIACEAE (Aricaceae): *Aralia.*
ERICACEAE: *Andromeda.*
CAPRIFOLIACEAE: *Sambucus.*
CUCURBITACEAE: *Cucurbita.*
COMPOSITAE: *Achaenites cichorioides.*

KEY TO THE POLLEN GRAINS OF THE FAMILIES OF THE LIVING REPRESENTATIVES OF THE GREEN RIVER FLORA[2]

A. Germinal apparatus consisting of a single pore or furrow, or rarely of two parallel furrows (MONOCOLPATE).
  I. Germinal apparatus consisting of a single furrow, more or less well defined, elongate.
    1. Provided with two lateral bladders.....Abietineae (M).[2]
    2. Not provided with lateral bladders.
      a. Furrow always long and narrow, not provided with an operculum.
        i. Grains 19–30μ long.....Arecaceae (M).
        ii. Grains over 50μ long.....Cabombaceae (Nymphaeaceae).
      b. Furrow usually broad and always provided with an operculum.....Nymphaeaceae (proper).
  II. Germinal apparatus a single more or less rounded or irregular-shaped pore.
    1. Pore small and round, slightly elevated and provided with an operculum; exine smooth.....Gramineae (M).
    2. Pore not elevated and not provided with an operculum.

[2] The pollen of some of the families and genera mentioned in the following key is not described further in the present work. These will be described and illustrated in the "Morphology of Pollen Grains," indicated by 'M.'

a. Exine reticulate, extremely thin; pore clearly defined.....Sparganiaceae.
b. Exine not reticulate, extremely thin; pore not clearly defined.
i. Grains in tetrahedral tetrads. Pore represented by a thin and elastic area of the exine.....Juncaceae (M).
ii. Grains not in tetrads. Pore represented by an irregular granular area or a group of small rifts in the thin exine.....Cyperaceae (M).

III. Germinal apparatus consisting of two elongate parallel furrows.....Pontederiaceae.

B. Germinal furrows or pores entirely absent, or represented only by scarcely visible and nonfunctional vestiges (ACOLPATE).

I. Intine thick, expanding when moist. Exine thin and transparent, grains spheroidal.
1. Exine flecked with granules of darkly staining material. Grains 25–30μ in diameter.....Taxaceae (Taxus) (M).
2. Exine conspicuously warty. Grains 75–105μ in diameter.....Musaceae. Cannaceae.
3. Exine covered with small sharp spines. Grains 25–65μ in diameter..Lauraceae.

II. Intine not excessively thick; exine not spiny or warty.
1. Grains single and ovoid, triangular or irregular in shape. Exine smooth or scurfy Cyperaceae (M).
2. Grains united in tetrads.....Juncaceae (M).
3. Grains united in flattened groups of 16, occasionally 8 or 32. Furrows vestigial, represented by slight linear depressions in the exine on the outer surfaces of the grain.....Mimosaceae (M).

C. Germinal apparatus consisting of three or more furrows or pores, or both, in which case the pores are enclosed by the furrows.

I. Furrows present, with or without pores, generally three but when more than three arranged in the trischistoclasic system (FURROWED GRAINS).
1. Furrows fully functional, generally three. Occasionally some of the grains may have more furrows arranged in the trischistoclasic system (TRICOLPATE).
a. Exine provided with well developed spines or vestiges of them, not bristly.
i. Exine without a lacunar pattern.
x. Spines short, conical and sharp pointed.....Astereae (M).
y. Spines greatly reduced or vestigial.....Ambrosieae (M).
ii. Exine with a well developed lacunar pattern (Echinolophate)..... Cichorieae (M).
b. Exine without spines or vestiges of them.
i. Exine reticulate or deeply pitted.
x. Reticulations coarse.
aa. Furrow membranes smooth. Grains more then 19μ in diameter.
AA. Reticulations isodiametric.....Vitaceae.
BB. Reticulations elongate.....Simarubaceae.
bb. Furrow membranes granular.
AA. Grains more than 20μ in diameter.
xx. Grains ellipsoidal or spheroidal.....Sterculiaceae.
yy. Grains flattened, triangular.....Araliaceae.
zz. Grains oblate spheroidal; some with four furrows..... Oleaceae (Fraxinus) (M).
BB. Grains less than 20μ in diameter.....Salicaceae (M).

y. Reticulations very fine, or exine merely pitted.
aa. With or without transverse furrow; exine pitted....Anacardiaceae.
bb. Without transverse furrows; exine reticulate.
AA. Pore sharply defined. Grains 17–26μ in diameter..Caprifoliaceae.
BB. Pore not sharply defined.
xx. Grains 16–35μ in diameter.....Celastraceae.
yy. Grains 35–45μ in diameter.....Cucurbitaceae (Ibervillea).
ii. Exine thick, coarsely pebbled in appearance, shading off to the finer texture of the stiff furrow membrane.....Aquifoliaceae (Ilex) (M).
iii. Exine faintly granular or quite smooth.
x. Grains more than 24μ in diameter.
aa. Without internal hyaline wedges.....Aceraceae.
Leguminosae.
bb. With three internal hyaline wedges, directed from the center of the grain towards the germ pores.....Fagaceae (M).
y. Grains less than 24μ in diameter, not provided with internal hyaline wedges.
aa. Grains decidedly oblately flattened, 17–18μ in diameter, with extremely large and clearly defined germ pores.....Crassulaceae.
bb. Grains spheroidal, ellipsoidal or only slightly flattened.
AA. Pores large and clearly defined.
xx. Transverse furrow present.....Castanea (M).
yy. Transverse furrow absent.....Ternstroemiaceae.
BB. Pores not clearly defined, represented only by a swelling of the furrow membrane.....Sapindaceae.
iv. Exine covered with closely packed fine bristles. Grains about 85μ in diameter.....Cucurbitaceae (Luffa).
2. Furrow reduced, scarcely or not at all functional in accommodating changes in volume, generally three.
a. Grains united in tetrahedral tetrads, with the furrows of adjacent grains contiguous and continuous across the sutures with those of their neighbors....
Ericaceae.[3]
b. Grains not in tetrads.
i. Furrows more or less deeply sunken pits, each almost coinciding in extent with its enclosed germ pore.
x. Exine provided with spines or vestiges of them.....
Ambrosieae (Ambrosia etc.) (M)
y. Exine not provided with spines.
aa. Grains about 35μ in diameter.....Tiliaceae (Tilia) (M).
bb. Grains about 20–25μ in diameter.....Myrtaceae.
ii. Furrows inconspicuous shallow streaks.....Rhamnaceae.
3. Furrows nonfunctional in accommodating changes in volume, not tapering, with broad rounded ends; always more than three, arranged in the trischistoclasic system.....Malpighiaceae.
II. Furrows, in the ordinary sense, absent, but pores present (PORED GRAINS).
1. Pores generally more than two.
a. Pores surrounded by a subexineous thickening (aspidate).

[3] Bowers (1931).

i. Pores protruding conspicuously, giving the grain an angular appearance.
x. Grains 11–23μ in diameter.....Moraceae.
y. Grains 20–30μ in diameter.....Betulaceae.
Myricaceae.

ii. Pores not protruding conspicuously.
x. Pores more or less crowded into one hemisphere.....Juglandaceae.
y. Pores not crowded into one hemisphere; generally three equally spaced around the equator, or a larger number irregular-distributed.....
Ulmaceae (Celtis).

b. Pores not surrounded by a subexineous thickening.
i. Pores more than 7 (generally 9–13), with opercula, not arranged around the equator. Grains spiny, 130–200μ in diameter.....
Cucurbitaceae (Cucurbita, Lagenaria).

ii. Pores 4–7 (occasionally 3), arranged around the equator, without opercula.
x. Grains oblate spheroidal, 25–35μ in diameter; pores elliptical.....
Ulmaceae (Ulmus and Planera).
y. Grains not oblately flattened, about 27μ in diameter; pores circular, surface warty.....Malpighiaceae (Heteropterys Gayana, Malpighia).

iii. Pores always three; grains flattened, and triangular or star shaped, about 33μ in diameter.....Proteaceae (Lomatia).

2. Pores always only two; grains crescent shaped.....Proteaceae (Banksia).

SPARGANIACEAE

The family comprises only the following genus. It is regarded as closely related to Typhaceae. This view is abundantly sustained by the similarity of their pollen-grain forms which amounts almost to identity except that, as far as I know, the grains of species of *Sparganium* never occur in tetrads, while those of at least one species of *Typha* (viz. *T. latifolia*) always occur in tetrads.

SPARGANIUM L. Grains spheroidal or somewhat irregular in shape, 22.8–23.9μ in diameter, with a single germ pore, approximately circular in outline, 2.8–5.7μ in diameter, its membrane bearing a few darkly staining flecks. Exine coarsely reticulate, rather thin, and collapsing irregularly without reference to the position of the germ pore, in spite of the stiffening effect of the reticulate thickening of the exine. Intine thick throughout and always a little thicker in the region immediately underlying the germ pore. These grains are virtually indistinguishable from those of *Typha angustifolia* L. which have been described elsewhere (M.[2]).

The genus comprises about 22 species of low marsh or pond herbs which are all rather closely related; widely distributed in temperate and cold regions. They are monoecious, and shed large amounts of light, airborne pollen, but less than that of *Typha*, to which they bear many resemblances.

SPARGANIUM ANDROCLADUM (Engelm.) Morong. (fig. 13). Grains as in the generic description.

Newfoundland to Minn., Fla. and La. June–Aug.

SPARGANIUM ACAULE (Beeby) Rydb. Grains as in the generic description, but may be distinguished from those of the preceding species by their slightly coarser reticulum.

In swamps and on muddy shores. Newfoundland to Iowa, S. Dak. and Va. July–Sept.

PONTEDERIACEAE

PONTEDERIA CORDATA L. (Fig. 17). Grains somewhat ellipsoidal in outline, about 45.5×48μ. Exine thick and rigid with a slightly granular texture. Furrows two, long, reaching almost from end to end of the grain. When the grain is expanded they are broad and of uniform width throughout their length, abruptly rounded at their ends; their membranes are smooth and sharply distinguished from the thick granular exine. The furrows are not diametrically opposite each other, but are displaced to one side of the grain, giving it a distinctly bilateral form in which a ventral and dorsal surface may be distinguished. The dorsal surface occupies nearly two thirds of the whole, arches throughout its length and projects laterally, overhanging the furrows and projecting beyond the margins of the ventral side, which is of smaller extent and less arched (fig. 8). The dorsal and ventral surfaces are separated from each other throughout most of their length by the two furrows but are joined to each other by a narrow isthmus at each end. The texture and thickness of the exine of dorsal and ventral surface is alike.

The presence of two furrows is certainly an anomalous condition among the grains of the Monocotyledons, since those of this group are predominantly monocolpate, unless acolpate by reduction. An explanation of this anomaly is offered by an analogous condition found among the grains of some of the Nymphaeaceae which are likewise characteristically monocolpate. In the grains of *Castalia* the furrow occupies the greater part of the ventral surface, but is almost entirely covered over by an extraordinarily large operculum. In most of the grains of this species this is not connected at any point to the exine of the general surface, being suspended and surrounded by a delicate furrow membrane. In a few grains, however, particularly those that are elongate in form, the operculum is connected with the exine of the general surface by a narrow isthmus at each end, thus dividing the encircling furrow membrane into two halves and giving them the appearance of two separate furrows. By analogy it therefore appears that in the grains of *Pontederia* the smaller ventral side is morphologically the operculum, and the two furrows represent the two halves of its encircling membrane. This interpretation is further substantiated by

the fact that in some grains of this species the isthmuses connecting the dorsal and ventral surfaces are extremely narrow and occasionally one of them even absent.

The Pickerel Weeds are semiaquatic herbs growing about the borders of ponds and streams, Nova Scotia to Minnesota, south to Florida and Texas. June–Oct. The genus includes about 8 species, native of America; while the family Pontederiaceae comprises about 5 genera and 25 species, inhabiting fresh water in the warm and temperate regions of America, Africa and Asia.

HETERANTHERA DUBIA (Jacq.) MacM. (*Schollera graminea* Gray). Grains similar to those of *Pontederia*, ellipsoidal, about 61μ long. Exine coarsely rough. The two furrows are similar to those of *Pontederia* in their curious one-sided arrangement and probably admit of the same interpretation, but differ from the latter in being covered completely over by exine of the same appearance as that of the general surface of the grain—they are merely longitudinal depressions.

Small aquatic plants with aerial flowers. Que. to Ore., south to Fla. and Mexico. July–Oct.

MUSACEAE

HELICONIA BIHAI L. (fig. 14 type). Grains entirely without furrows or pores, when fully expanded spherical, about 75–85μ in diameter. Exine exceedingly thin and transparent, but covered with numerous small opaque wart-like projections. Intine exceedingly thick and transparent, but in optical section exhibiting a radially striate appearance. This form of grain bears a remarkably close resemblance to that of the Lauraceae (q. v.).

A striking plant resembling the cultivated banana. West Indies, Central and South America. The genus includes 30 or 40 species in the American tropics, sometimes planted for their large banana-like foliage.

MUSA PARADISIACA var. SAPIENTUM Ktze. (*M. sapientum* L.). Grains similar to those of the type, except that the intine is less thick and swells less when moistened; 94–102μ in diameter; a large proportion of the grains are abortive and empty.

A tall plant, 10–30 ft. high with drooping spikes of fruit, native of India but widely cultivated in tropical countries. The genus includes 50 or more species native in the tropics of the Eastern Hemisphere.

CANNACEAE

CANNA GENERALIS Bailey. Grains similar to those of the *Heliconia* type, but with the wart-like protuberances of the exine more prominent and almost spine-like, about 1μ high and about 11μ apart. Grains 75–90μ in diameter, with the intine 15–22μ thick.

The common garden Canna, exists in many varieties which are the result of hybridization and breeding. The genus contains about 50 species of wide distribution in the Western Hemisphere. It is the only genus of the family Cannaceae, and is regarded as being closely related to the Musaceae.

CABOMBACEAE (Nymphaeaceae in part)

Grains long-ellipsoidal, monocolpate, 57–87μ long, and when fully expanded, about two thirds as broad. The furrow reaches almost the entire length of the grain; when expanded it is rather broad, with rounded ends and not tapering, often contorted and asymmetrically placed. Its membrane is either granular and broken by irregular rifts, or apparently lacking. When dry the furrow is tucked deeply in and appears as a narrow groove. In this condition the grain is only about one half of its expanded width, but is of the same length. Exine rather thick and stiff, often splitting longitudinally on the dorsal side, its surface granular or marked by conspicuous striae.

Aquatic perennial herbs, with both submerged and floating leaves and aerial flowers. Two genera and about five species of wide distribution in fresh-water lakes and streams. These two genera are frequently regarded as belonging to the Nymphaeaceae, and indeed are treated as such by Knowlton. But the form of their pollen grain bears no resemblance to those of the Nymphaeaceae, beyond being monocolpate, and therefore suggests that no relation really exists between the families. Or possibly they are both derived as separate stocks from the Bennettitales.

BRASENIA SCHREBERI Gmel. (*B. peltata* Pursh). fig. 19. Grains ellipsoidal, about 46×57μ; the single furrow generally asymmetrically placed and more or less contorted, without a well developed furrow membrane, appearing as an expanded rift through the exine. Exine finely granular, occasionally the granules tending to be linearly arranged, fragmented along the margins of the furrow. Intine thick throughout and thicker in the region underlying the furrow.

An aquatic herb with floating leaves and aerial flowers; in slow streams and ponds. Nova Scotia to Fla., Man., Neb. and Tex. also in Cuba and Mexico, and on the Pacific coast.

CABOMBA AQUATICA Aubl. Grains similar in general form to the *Brasenia* type; somewhat various in size, as if a large proportion of them were defective. Normal grains, when fully expanded, about 49×73μ; furrow broad, straight or contorted, with its membrane composed of coarse granules. Exine rather firm, markedly striate with longitudinal granular striae. When dry the furrow is tucked in tightly and deeply, causing the grain to assume an extremely elongate form. Mexico.

CABOMBA CAROLINIANA Gray. Grains indistinguishable from those of *C. aquatica*.

In ponds and slow streams. Mo. to Ill. to N. C. and south to Fla. and Tex. May–Aug.

MYRICACEAE

COMPTONIA PEREGRINA Coult. (*Myrica asplenifolia* L.) figs. 11, 16. Grains similar to those of birch, about 27μ in diameter, generally with three pores equally spaced around the equator, but extremely variable in this respect; frequently with two to five pores irregularly arranged, often all crowded into one hemisphere. Germ pores aspidate with their apertures circular or somewhat elliptical, 3.5μ in diameter. Texture nearly or quite smooth, or faintly granular around the pores.

A monoecious aromatic shrub. Nova Scotia to Man., Mich., Ind., Tenn. and N. C. Flowers in spring shedding large amounts of air-borne pollen. The family comprises about 35 species of shrubs or small trees of wide distribution in warm and temperate regions almost throughout the world.

MYRICA GALE L. Grains essentially as in *Comptonia peregrina*.

A small dioecious shrub along streams and ponds Newfoundland to Alaska, southern N. Y., Va., Mich. and Wash. Also Europe and Asia. Wind pollinated. April and May.

LAURACEAE

The grains of this family, as far as these observations have gone, are characterized by their lack of pores or furrows, the enormous thickening of their intine and the thinness of their exine which bears numerous characteristic spines. In size they range from about 25–65μ in diameter.

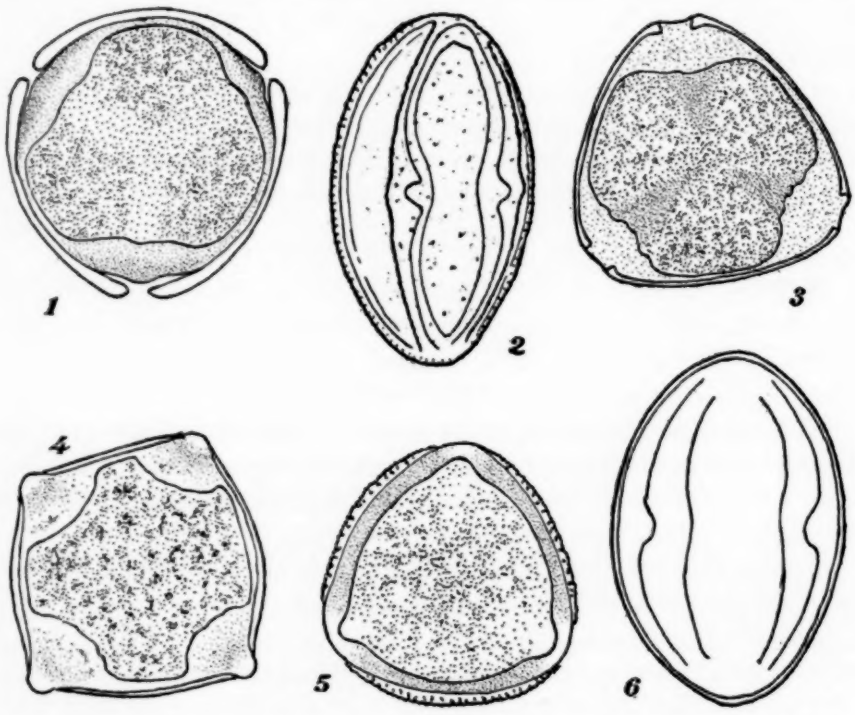
The family comprises about 1000 species, in about 40 genera, of trees and shrubs of wide distribution, principally in the tropics.

1. Grains 25–35μ in diameter, spines 2–3μ apart.
   i. Grains 25–30μ in diameter; intine about 3μ thick, and spines about 2.3μ apart.... *Ocotea flavescens.*
   ii. Grains 31–35μ in diameter, intine about 4μ thick, spines about 2.4μ apart..... *Benzoin aestivale.*
2. Grains 48–64μ in diameter; spines 4.6μ apart.
   i. Intine about 9μ thick, spines about 5.7μ apart..... *Laurus nobilis.*
   ii. Intine about 15μ thick, spines about 4.6μ apart..... *Persea americana.*

BENZOIN AESTIVALE (L.) Nees. (*Laurus aestivalis* L.) fig. 29. Grains, when moist, nearly or quite spherical, 32–33μ in diameter. Exine extremely thin and transparent, but bearing numerous small deeply staining conical spines, about 2.5μ apart, and very faint lines dividing its surface into polygonal areas, each occupied by a spine at its center. Intine thick and transparent, swelling when moistened to about 4μ in thickness.

This character gives these grains a remarkable resemblance to those of *Heliconia* and allied species and to a lesser extent to those of the Cupres-

sineae and Taxodineae. They may be distinguished, however, from the former by their smaller size, their pointed spines and the fact that the intine instead of presenting a radially striate appearance in optical section, appears to be made up of faintly distinguishable concentric layers. And from the Taxodineae and Cupressineae they are easily distinguished by their small spines instead of the flecks which characterize the latter. When dry these grains shrink without distortion to about 24μ in diameter. The



Figs. 1–6. 1. Pollen grain of *Eucalyptus diversicolor*, transverse optical section; 2. Pollen grain of *Rhus glabra*, longitudinal section of a grain that is collapsed and empty; 3. Pollen grain of *Zizyphus Jujuba*, transverse optical section; 4. Pollen grain of *Comptonia peregrina*, a grain with four pores, seen in transverse optical section; 5. Pollen grain of *Ailanthus glandulosa*, transverse optical section; 6. Pollen grain of *Parthenocissus hirsuta*, longitudinal optical section.

major portion of the change is accomplished by the intine for in this condition it measures only about 1.7μ in thickness.

The forms of both this grain and that of *Heliconia* are obviously reduced, and their resemblance to each other is one of the most remarkable examples of convergence I have yet encountered among pollen-grain forms. Since *Heliconia* is a rather typical Monocotyledon, the form of its grain

is presumably derived from the one-furrowed type which characterizes the Monocotyledons. On the other hand since *Benzoin* is a rather typical Dicotyledon, the form of its grain is presumably ultimately derived from the three-furrowed type of grain which characterizes the Dicotyledons. The remarkable form of these two types of grains and that of the Cupressineae and Taxodineae is probably the result of some unexplained environmental stimulus, and deserves further investigation.

PERSEA AMERICANA Mill. (*P. gratissima* Gaert.) Grains essentially as in *Benzoin*. When moist, about 50–64μ in diameter, depending somewhat upon the extent of the expansion of the intine which, when fully expanded, is generally about 15μ thick, considerably thicker than in the grains of *Benzoin*. Spines small, about 4.6μ apart.

A large tree, attaining a height of about 60 feet. Native of tropical America, now much cultivated in California, and to a certain extent in Florida and elsewhere in the warm parts of the U. S. A. for its edible fruit. Insect pollinated. Flowers in spring.

LAURUS NOBILIS L. Grains essentially as in *Benzoin*. When expanded 48–57μ in diameter, depending somewhat upon the extent of the expansion of the intine which is generally about 9μ thick. Spines rather large and each obviously sunk in a little pit (fig. 15), about 5.7μ apart. The exine, though nearly transparent, when properly stained, can be seen to be slightly granular.

A small evergreen tree with stiff leaves and inconspicuous yellowish axillary flowers in early spring. Native of the Mediterranean region. Now much cultivated as a tub plant. The genus contains only one other species which is native of the Canary Islands.

OCOTEA FLAVESCENS Rusby. Grains essentially as in *Benzoin*, 26–30μ in diameter when moist; intine about 3μ thick, spines about 2.3μ apart. A tree about 50–60 feet high, common in mountain forests near Valparaiso.

The genus comprises about 200 species, principally from subtropical America.

CRASSULACEAE

These are mostly herbs and shrubs. There are about 900 species in 20 genera which are of wide distribution and frequently cultivated in rock gardens.

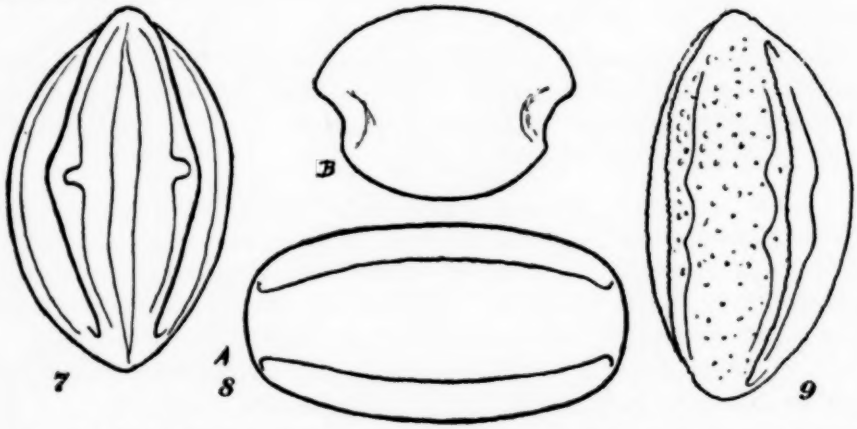
SEDUM L. Grains, when expanded, oblately flattened, rounded triangular in outline when seen in polar view, about 17.1×16μ. Furrows three, situated at the angles of the grain, long and tapering to sharply pointed ends, gaping widely open when expanded. Furrow membranes smooth; germ pore large and bulging prominently out through its germinal aperture. Exine rather thin, but apparently rigid; texture quite smooth. Collapsed grains are ellipsoidal,

about 16×20μ, with the furrows tucked tightly into narrow longitudinal grooves through which the pores are scarcely discernible from the surface (fig. 7). Many abortive and dwarf grains are found which are collapsed and measure about 14.8×16.5μ.

A genus comprising about 200 species of fleshy herbs, native of temperate and cold regions of the northern hemisphere, Mexico and the Andes of South America.

SEDUM ACRE L. (figs. 18, 20). Grains as in the generic description.

Densely tufted perennial, on rocks along roadsides and in gardens. Native of Europe and northern Asia, but extensively introduced into America. June to August.



Figs. 7–9. 7. Pollen grain of *Sedum Nuttallianum*, about 16×20μ, empty and collapsed, to show the change in form that takes place in *Sedum* grains when the cell contents is dissolved away; 8. Pollen grains of *Pontederia cordata*, diagramatic, A, ventral view and B, end view to show the position of the two furrows; 9. Pollen grain of *Ibervillea Lindheimeri*, optical section of a collapsed grain.

SEDUM NUTTALLIANUM Raf. Grains indistinguishable from *S. acre*, but a small proportion of them show four and six furrows arranged in the trischistoclasic system.

A low tufted annual in dry open places. Mo. to Ark. to Tex. May.

SIMARUBACEAE

There are about 150 species in 30 genera, represented by trees and shrubs of wide distribution in tropical and warm regions.

AILANTHUS GLANDULOSA Desf. (*A. altissima* Swingle). fig. 33. Grains, when moist, oblately flattened, 25–26.5μ in diameter; when dry ellipsoidal, about 20–25.1μ in diameter (fig. 5), tricolpate with long tapering furrows; furrow membranes smooth; germ pores moderately large, circular and clearly

defined. Exine rather thick and coarsely reticulate with the reticulations tending to be linearly arranged.

A rapid-growing tree. Native of China, naturalized in eastern North America, commonly planted as a shade tree. The genus includes about 10 species in Asia and northern Australia.

MALPIGHIACEAE

The grains of the Malpighiaceae are characterized by a tendency towards an increase in the number of their pores and furrows, together with a reduction in their length and definition. All stages may be found from the ordinary tricolpate form with three pores in three well marked furrows, through that with a large number of well developed pores associated with a still larger number of sketchy furrows, to others in which the furrows have entirely disappeared. Such a condition is not unusual in the pollen of other families. It is found in that of the Polygonaceae (Wodehouse '31), and probably represents a stage in the evolution which leads to the many pored furrowless forms, such as those of the Chenopodiaceae and Cucurbitaceae. One outstanding character of the grains of the Malpighiaceae which I have not observed elsewhere, is that the pores tend to be at the ends of the furrows, instead of at the middle.

The family comprises about 650 species of trees, shrubs and woody climbers, of wide distribution in the tropics, particularly the tropical forests of South America, represented in the U. S. A. by *Byrsonima*, *Malpighia*, *Thryallis* and *Aspicarpa*.

I. Furrows clearly defined and generally arranged according to the trischistoclasic system.
  1. Furrows six to twelve, pores 4–6, generally at the ends of the furrows; grain 29–35μ in diameter.
    i. Grains 29–35μ in diameter ..... *Heteropterys cornifolia.*
    Banisteria leptocarpa.
    ii. Grains 45–58μ in diameter
      a. Furrows generally 12, distinct ..... *Gaudichaudia Schiediana.*
      Gaudichaudia pentandra.
      b. Furrows various in number, poorly defined .... *Gaudichaudia Karwinskiana.*
  2. Pores generally at the centers of their furrows.
    i. Furrows characteristically four ..... *Heteropterys Beecheyana*
    ii. Furrows more than four, various ..... *Heteropterys acutifolia.*
II. Furrows entirely absent; pores generally four ..... *Heteropterys Gayana.*
III. Furrows present but very irregular and not conforming to the trischistoclasic system; pores 6–12 ..... *Malpighia Harrisii.*
Malpighia punicifolia.
Malpighia urens.

GAUDICHAUDIA H. B. K. Grains when expanded almost perfectly spherical, 47–57μ in diameter; when dry, cubical and somewhat smaller, furrows

always 12, excepting in *G. Karwinskiana*, and symmetrically arranged in the ordinary dodecacolpate configuration, shallow, of uniform width throughout their length, rounded at their ends, and with slightly notched or wavy margins; furrow membranes slightly flecked with small granules. Pores six, circular in outline, about 5.7μ in diameter and always at the ends of the furrows which they occupy, and so distributed that there is never more than one pore placed near a triradiate center of convergence, and two of the eight centers are without pores near them. If the grain be so oriented that one of the poreless centers is uppermost, the three furrows which radiate from it each has a pore at its distal end. The other poreless center is exactly opposite on the other side of the grain with its three radiating furrows bearing pores at their distal ends, and alternating with those of the upper center. The remaining six furrows, none of which is occupied by a pore, zigzag across the limb of the grain, converging towards the pores of the two opposite groups. Exine smooth and thin. Intine about 4.5μ thick.

The genus comprises about 12 species of shrubs, commonly climbing, principally in Mexico, with a few in Venezuela and Brazil, though the latter are generally regarded as belonging to the genus *Janusia* Juss.

GAUDICHAUDIA SCHIEDIANA Juss. (fig. 30). Grains as in the generic description, with the furrow pattern always regular and extremely uniform.

Native of Mexico, bearing yellow flowers. Nov.–April.

GAUDICHAUDIA PENTANDRA Juss. Grains exactly as in the type .

Native of Mexico.

GAUDICHAUDIA KARWINSKIANA Juss. Grains mostly similar to the type, but less uniform. Some have furrow configurations corresponding to the dodecacolpate configuration, but with one or more furrows missing and some have larger numbers of pores, up to twelve, introducing various irregularities into their furrow patterns.

Native of Mexico.

HETEROPTERYS Juss. Grains various in the different species.

The genus comprises about 90 species or shrubs, occasionally climbing, principally of southern Brazil and Bolivia, but with a few species ranging northward to Mexico, and a single species, *H. africana*, on the west coast of tropical Africa.

HETEROPTERYS ACUTIFOLIA Juss. Grains various; when moist and expanded, spheroidal, 30–31.5μ in diameter, resembling those of the *Gaudichaudia* type, except in the number and arrangement of their pores and furrows, which are here extremely various. For example there may be 9 furrows and 6 pores, 6 furrows and 5 pores, or 6 furrows and 6 pores. The pores are always at the centers of the furrows which they occupy. Nevertheless the furrows are

generally symmetrically arranged in the trischistoclasic system, though occasionally two furrows may be fused at one or more of the centers of convergence, suggesting in appearance a single long furrow occupied by two pores. Furrow membranes smooth or flecked, margins of the furrows jagged. Pores circular in outline, 2.8–3.4μ in diameter, surrounded by a subexineous thickening which causes them to protrude slightly above the surface of the furrow. Pore membranes smooth; exine rather thick and warty.

A little known species in northern Brazil.

HETEROPTERYS CORNIFOLIA H. B. K. Grains rather uniform; when moist, spheroidal, 28.5–30.5μ in diameter. Furrows generally 9 arranged in the usual nonacolpate configuration, similar in structure to those of *Gaudichaudia*, their membranes granular. Pores generally six and generally at the ends of their furrows, circular in outline, about 5.7μ in diameter, surrounded by an annular thickening which causes them to protrude slightly above the surface of the furrow. Exine smooth or somewhat granular.

HETEROPTERYS BEECHEYANA Juss. Grains similar to those of *H. acutifolia*, but somewhat various, a large proportion abortive and dwarf. Normal grains, when moist, 36.5–40μ in diameter. Furrows always 4, in the ordinary tetracolpate configuration, and with 4 pores which are generally at the centers of the furrows. Furrows of medium length and tapering to sharp pointed ends; germ pores circular in outline, about 6.5μ in diameter, sharply defined and protruding slightly above the surface of the furrow. Exine rather thin.

A shrub in dry savannas, native of Mexico.

HETEROPTERYS GAYANA Juss. Grains somewhat various, with a large proportion abortive; when expanded, spheroidal in form and 36.5–38μ in diameter. Pores 4, circular in outline, each surrounded by a subexineous thickening causing it to protrude rather prominently above the surface of the grain, 3.5–4μ in diameter. Furrows absent. Exine rather thick and warty.

Native of Mexico.

BANISTERIA LEPTOCARPA Benth. Grains similar to the *Gaudichaudia* type, somewhat various and with a small proportion of them obviously abnormal. Normal grains, when moist, spheroidal in form, 32–33.1μ in diameter, when dry they become polyhedral with the furrows lying along the edges, and in this form measure about 30μ in diameter. Furrows mostly 6, 9 and 12, occasionally other numbers, generally beautifully symmetrical in the trischistoclasic system; in form they are very shallow and faint and do not taper towards their ends; their edges are jagged and their membranes flecked with granules. Pores circular, about 7.5μ in diameter, fewer than the furrows, each at the end of the furrow it occupies, and occasionally there are two pores in the same furrow, one at each end. Exine rather thin, finely and faintly granular.

MALPIGHIA L.—Grains similar to the *Gaudichaudia* type, but with a vari-

able number of pores and furrows, the latter often extremely irregular in arrangement, very faint or even altogether lacking.

The genus comprises about 20 species of trees and small shrubs, principally in Mexico and the West Indies, also in the Bahamas and South America to Peru and Brazil.

MALPIGHIA URENS L. Grains spheroidal, 30–33μ in diameter. Furrows very irregular, not arranged in the trischistoclasic system, frequently fused at one or more of their centers of convergence. Pores generally six, circular, 3.4μ in diameter. Exine thin and broken by a number of irregular rifts, sometimes merging with and scarcely distinguishable from the furrows.

Native of the Antilles.

MALPIGHIA HARRISII Small. Grains similar to the preceding, 35–38μ in diameter. "This species appears to be most closely related to *M. urens*." A slender shrub. Jamaica.

MALPIGHIA PUNICIFOLIA L. (*M. biflora* Poir.). Grains spheroidal, 47–53μ in diameter. Pores 6–12 in number, irregularily arranged, 6–8μ in diameter. Furrows entirely absent or represented by faint and irregular markings in the exine which is very thin, possibly too thin to support a clearly defined furrow.

Tropical America.

CELASTRACEAE

The family comprises about 400 species of trees and shrubs or occasionally climbers, distributed throughout the warmer parts of the world.

CELASTRUS SCANDENS L. (fig. 32). Grains uniform, 21–24μ in diameter, spheroidal or slightly flattened, according to the degree of their expansion. Furrows three, sharply defined, long and tapering to slightly rounded ends, their membranes slightly granular, especially around the pores which are rather large and somewhat elongate in the meridional direction. Exine rather heavy and coarsely reticulate.

A climbing shrub with unarmed twining branches, bearing orange and scarlet fruits in autumn; along streams, thickets and fences Que. to Man. south to Ga. Flowers in spring, insect pollinated.

MAYTENUS Molina. Grains uniform, spheroidal, 16–17.1μ in diameter, tricolpate with furrows long and tapering to pointed ends. Furrow membranes smooth, germ pores circular. Exine rather thin, but conspicuously, though finely, reticulate pitted. This grain differs from the *Celastrus* type in its smaller size, finer pitting of the exine and the rounded shape of its pores.

About 120 species of evergreen trees and shrubs, tropical and temperate South America and West Indies. Some species are cultivated for their attactive foliage and fruit.

MAYTENUS ELLIPTICA (Lam.) Krug. & Urb. Grains as in the generic description.

A tree attaining 36 feet, in the forests of Porto Rico.

MAYTENUS TETRAGONUS Griseb. Grains indistinguishable from those of the preceeding species.

Native of the West Indies.

EUONYMUS AMERICANUS L. Grains various, a large proportion irregular, dwarf and abortive. Normal grains generally tricolpate, occasionally tetracolpate, oblately flattened, about 27–31μ in diameter. Furrows long and tapering with their membranes smooth; germ pores round and rather large, about 8μ in diameter. Otherwise similar to the type.

A small to medium sized shrub, partly trailing, on river banks, N. Y. to Ill. Fla. to Ark. Tex. Flowers in summer.

SAPINDACEAE

There are about 125 genera and more than a thousand species of trees and shrubs, often climbing. They are of wide distribution in the tropics and warm regions.

SAPINDUS L. Grains mostly tricolpate, but generally a few with 6 or 9 furrows, somewhat various. Normal grains oblately flattened, 16–20μ in diameter, triangular in outline, with the furrows at the angles. Furrows long and tapering, their membranes smooth and without well defined germinal apertures, the germ pore marked only by a slight swelling. Exine thin, slightly granular or quite smooth.

The genus contains about 15 species of trees and shrubs, native of the tropics.

SAPINDUS MARGINATUS Willd. (fig. 31). Grains as in the generic description.

In low and sandy soil. So. Carolina and Ga. to Fla. Flowers in spring.

SAPINDUS DRUMMONDII Hook & Arn. Grains indistinguishable from the preceding.

In dry soil. Kans. to Ark. La. and Ariz. Also in Mexico. Flowers in spring.

TALISIA Aubl. Grains rather uniform, oblately flattened and somewhat angular in outline when expanded, 21–29μ in diameter, 3- or occasionally 4-colpate with furrows long and tapering, rather vaguely defined, and with their membranes smooth. Germ pores relatively large, elongate in the meridional direction. Exine thin and of smooth texture, merging almost imperceptibly into that of the furrow membrane, so that the boundary of the latter is poorly defined.

About 33 species of small trees in tropical America.

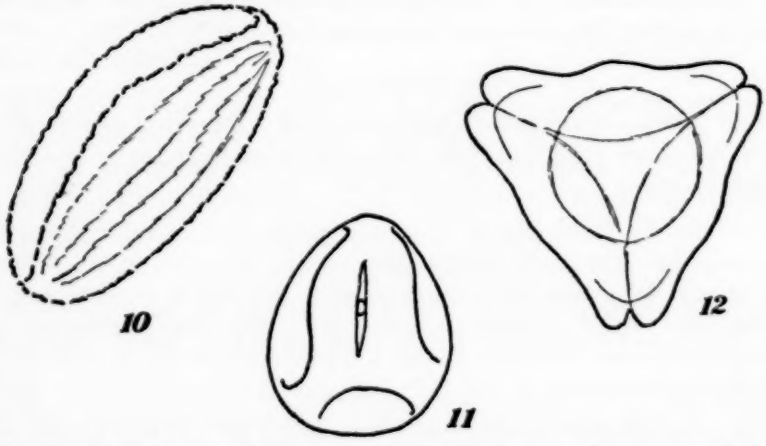
TALISIA OLIVAEFORMIS Radlk. Grains prevailingly 3-colpate, but with a fair proportion 4-colpate, 21.5–23μ in diameter, otherwise as in the generic description.

Yucatan, British Honduras, Colombia, Venezuela and Trinidad.

TALISIA DEPRESSA Pitt. (fig. 27). Grains 3-colpate, rarely, if ever, with higher numbers of furrows, 23.5–28.5μ in diameter. Otherwise as in the generic description. Venezuela.

ANACARDIACEAE

There are about 60 genera and 400 species of shrubs which are most abundant in the tropics.



Figs. 10–12. Empty and collapsed pollen grains, as seen by transmitted light, to show their mode of shrinking. It is in such condition that they are most likely to be encountered in fossil material. 10. *Parthenocissus hirsuta*, side view with one furrow showing to the left; 11. *Zizyphus Jujuba*, side view; 12. *Eucalyptus diversicolor*, polar view.

RHUS L. Grains when fully expanded ellipsoidal or spheroidal, 33–39μ broad, tricolpate with long and sharply defined furrows tapering to slightly rounded ends. Furrow membranes slightly flecked with fine granules. Germ pores about 3–4μ in diameter, emerging through a transverse furrow which is sharply outlined by an inwardly projecting ridge. Exine heavy, finely reticulate pitted or occasionally granular. The genus includes about 150 species of trees or shrubs.

Native to temperate, tropical and subtropical regions of both hemispheres.

RHUS GLABRA L. (*Schmaltzia glabra* (L.) Small.) fig. 36. Grains when fully expanded ellipsoidal, 35.3–40μ, when collapsed 25.1$\times$41μ (fig. 2). Exine ex-

tremely finely pitted, sometimes appearing simply granular. Otherwise as in the generic description.

A shrub in dry soil and thickets, N.S. to B.C., Fla. to Miss. and Ariz. Spring and summer.

RHUS TYPHINA L. (*R. hirta* Sudw., *Schmaltzia hirta* (L.) Small.) Grains spheroidal or slightly ellipsoidal, 37.5–39 μ in diameter. Exine finely but conspicuously reticulate. In these two characters easily distinguished from the type.

A shrub or small tree in rocky soil. N. B. to Ont. Minn. Ga. and Miss. Spring and summer. Insect pollinated but shedding large quantities of pollen.

SPONDIAS MOMBIN L. (*S. lutea* L.) Grains similar to the *Rhus* type, long ellipsoidal, 34–39μ broad and 43–50μ long. Furrows long and tapering to sharp pointed ends. Furrow membranes smooth or only very slightly flecked with granules. Germ pore 8μ in diameter, broader than the furrow and forcing it apart as it bulges through, but not provided with a transverse furrow. Exine coarsely reticulate pitted, with the pits elongate and linearly arranged in a meridional direction. This grain is easily distinguished from that of *Rhus* by its more elongate form, the coarser pitting of the exine and absence of transverse furrows.

A tree attaining 25 feet in height. Tropical America. Frequently cultivated.

RHAMNACEAE

The family comprises about 600 species in 50 genera, of trees and shrubs of wide distribution.

ZIZYPHUS JUJUBA Lam. (*Z. sativa* Gaert., *Z. vulgaris* Lam.) figs. 3, 35. Grains decidedly flattened and triangular in outline, 21.5–23μ in diameter, with their germinal apertures, one at each angle. Pores elliptical, 3.4μ long, elongate in the meridional direction; tricolpate, but the furrows are represented by only very shallow streaks which are frequently scarcely visible. Each pore is surrounded by a weakly developed subexineous thickening which gives it an aspidate appearance. Exine thin and smooth.

A shrub or small tree, native of southern Europe, and southern and eastern Asia. Cultivated elsewhere.

ZIZYPHUS SONORENSIS Wats. Grains indistinguishable from the type.

A shrub, native of Mexico.

VITACEAE

The family comprises about 500 species in 12 genera, mostly tendril-climbing woody vines, though there are also included in it some erect

shrubs and even small trees. Principally of the tropics and warm temperate regions.

PARTHENOCISSUS HIRSUTA (Donn) Graebn. figs. 6, 34. Grains, when expanded, 30×40μ. Tricolpate with furrows long and tapering; furrow membranes smooth, provided with well marked germinal apertures, 4.6μ broad. Exine thick and conspicuously reticulate, with the network most open towards the centers of the lunes, closer towards the poles and along the margins of the furrows.

A spreading, tendril-climbing vine. Ga. to Tex. and Mexico. Spring.

PARTHENOCISSUS QUINQUEFOLIA (L.) Planch. (*Ampelopsis quinquifolia* (L.) Michx.) Grains essentially the same as the type, except that they are somewhat less elongate.

A strong high-climbing woody vine. Native of eastern North America. Spring. The genus comprises about 12 species of woody tendril-climbers, Native of North America and Asia.

VITIS VINIFERA L. Cultivated Grape. Grains extremely irregular and various in form and size. Normal grains 19–22μ in diameter, prevailingly tricolpate, but a large proportion have 4 or 6 furrows, either regularly arranged in the trischistoclasic system, or variously irregular. Furrows poorly defined, their membranes smooth; germ pores round. Exine very thin, much thinner than in the grains of *Parthenocissus*, but faintly reticulate.

STERCULIACEAE

The family includes about 750 species in 10 genera, of plants of all forms, throughout the tropics of both hemispheres. It is of particular interest because it contains *Theobroma Cacao*, the source of chocolate, and *Cola acuminata*, the Cola Nut.

STERCULIA L. Grains always uniform, slightly ellipsoidal to spheroidal, depending upon their degree of expansion, about 30.4×33.5μ; tricolpate with furrows sharply defined, long and tapering, their membranes flecked with granules. Germ pores sharply defined and somewhat elongate in a transverse direction. Exine very coarsely reticulate but with low ridges.

About 60 species of trees in the tropics of both hemispheres, but mostly in the East Indies and Malay Archepelago.

STERCULIA APETALA (Jacq.) Karst. (*S. carthaginensis* Cav.) fig. 23. Grains as in the generic description.

Tropical America.

STERCULIA MEXICANA R. Br. Grains indistinguishable from the type. Mexico.

STERCULIA FOETIDA L. Grains indistinguishable from the type. Cuba.

TERNSTROEMIACEAE

There are about 175 species in 16 genera of trees and shrubs, native of tropical and subtropical regions throughout the world.

TERNSTROEMIA GRANULATA Kr. & Urb. (fig. 22). Grains uniform, ellipsoidal when expanded, 16–18.2μ in diameter; tricolpate with furrows long and tapering, their membranes smooth. Germ pores large, bulging prominently through their apertures, about 5.5μ in diameter. Exine thin and perfectly smooth. A small tree, native of Jamaica. May–Sept. with white fragrant flowers.

The genus, also known as *Taonabo* Aubl., comprises about 30 species of evergreen trees and shrubs in tropical America and Asia.

PROTEACEAE

The family comprises about 1000 species in 50 or more genera, of trees and shrubs, native of Australia, South Africa, tropical eastern Asia and tropical South America.

LOMATIA ILICIFOLIA R. Br. (fig. 26). Grains decidedly flattened and triangular or triradiate in outline, about 33μ in diameter, with three pores without furrows, each situated at the end of a horn-like projection. Germinal apertures approximately circular in outline; pore membrane generally provided with a single central fleck. Exine lightly marked with a very slightly raised reticulum.

LOMATIA OBLIQUA R. Br. Grains indistinguishable from the type.

A shrub or small tree native of Chile.

BANKSIA L. f. Grains always uniform, two-pored, elongate and arched, with one pore at each end, about 51$\times$24.5μ. Pores circular, about 8μ in diameter, surrounded by a slightly thickened collar of the exine. Exine smooth or faintly granular.

The peculiar form of these grains with their projecting germ pores, as compared with those of *Lomatia*, suggests that this form may be a two pored derivative from the *Lomatia* type. They further differ, however, in their smooth texture and larger size.

This unusual and striking form of pollen grain, besides being common to the two species of *Banksia* here described, according to Francis Bauer[4]

[4] Francis Bauer, F.R.S. 1758–1840. Drawings of about 215 species of pollen grains, unpublished, are deposited in the British museum (Natural History). The majority of these are in the form of unfinished sketches, though a few are beautifully finished in natural colors. He appears to have left no notes, other than their names and occasional brief descriptive sentences to facilitate the completion of the drawings, but these, together with the drawings, both completed and unfinished, show an understanding of pollen grains many years in advance of his time.

also characterizes that of *Banksia media, B. Cunninghamia, B. marginata, Dryandra floribunda* and *D. formosa*. It thus appears that this grotesque form is firmly established in the family, and is not due merely to some individual or specific anomaly in the arrangement of the pollen cells in their tetrads as the form suggests. Its origin in relation to tetrad formation, certainly deserves further study.

The genus comprises about 45 species of trees and shrubs, exclusively Australian. Flowers extremely small, 500 to 1000 tightly compacted in a large brush-like head.

BANKSIA CANDOLLEANA Meissn. (fig. 21). As in the generic description. Sand plains of western Australia.

BANKSIA PROSTRATA R. Br. type. Grains as in the type, except that their form is slightly more arched, and their exine slightly more granular, especially around the pores.

MYRTACEAE

The family comprises about 3000 species in 72 genera, of trees and shrubs, native in the tropics, particularly of America and Australia.

EUCALYPTUS L'Her. Grains rather uniform, except for a large proportion that are abortive, generally flattened and triangular in outline, about $25 \times 19\mu$. Germinal furrows three, one at each angle, extremely short, each consisting of an elongate and rather vaguely defined depression in the exine with its major axis directed meridionally; it is crossed by a rather conspicuous transverse furrow. The area where the latter underlies the former constitutes the germinal aperture and is rather small. Neither the pore nor the furrow of these grains functions in accommodating volume changes. This function is obviously taken over by the flattened polar surfaces which by becoming more or less arched can easily compensate for any increase or decrease in size. The pores are surrounded by a rather conspicuous subexineous thickening which gives them an almost aspidate appearance. Exine rather thick and perfectly smooth.

The genus comprises about 300 species of mostly tall trees, native of Australia and the Malayan region.

EUCALYPTUS DIVERSICOLOR F. M. (fig. 25) type. Grains as in the generic description.

A tall tree native of western Australia, cultivated in California.

EUCALYPTUS ROBUSTA J. E. Smith. Grains essentially as in the type.

A tall tree, cultivated in California.

ARALIACEAE

There are about 500 species in 50 genera, herbs shrubs and trees of wide distribution.

ARALIA SPINOSA L. (fig. 24). Grains when moistened decidedly flattened and triangular in outline, 25–30μ in diameter; when dry they tend to become more flattened and more triangular; tricolpate with furrows of medium length and tapering to sharp points. Furrow membranes always ruptured when expanded, marked by a faint centrally placed granular streak. Germ pores large and bulging prominently Exine rather thick and conspicuously reticulate but somewhat finer towards the margins of the furrows.

A tall shrub or tree attaining a height of 30 ft. So. Pa. to Mo. and Fla. "Frequently planted for the oddity of its thick club-like branches" which suggest its English name Hercules Club. The genus comprises about 40 species of herbs, shrubs and trees, native of Asia, Malaya, Australia and North America.

CAPRIFOLIACEAE

The family comprises about 350 species of trees shrubs and vines, principally of the north temperate zone, a few in the mountains of the tropics.

SAMBUCUS L. Grains uniform, spheroidal or somewhat ellipsoidal, depending upon the degree of their expansion, 17–26μ in diameter, tricolcolpate, with furrows very long, in one species sometimes meeting at the poles, their membranes smooth, each with a large bulging germ pore with poorly defined margins. Exine conspicuously reticulate throughout, except towards the margins of the furrows where it merges with their smooth membranes, with slight differences in the different species.

The genus comprises about 20 species of shrubs and small trees in temperate and subtropical regions of both hemispheres.

SAMBUCUS CANADENSIS L. (fig. 28) type. Grains as in the generic description, about 18μ in diameter; furrows of medium length, not joined at the poles. Exine finely reticulate.

A large shrub producing cymes of showy white flowers in June and July. N. S. and Man. to Fla. and Tex.

SAMBUCUS PERUVIANA L. Grains essentially as in the type, about 21.6μ in diameter. Exine more coarsely reticulate.

Shrub, native in tropical and subtropical America.

SAMBUCUS NIGRA L. Grains similar to the type, about 17.1μ in diameter. Furrows frequently all three, or sometimes two of them, united at the poles. Exine finely reticulate.

A shrub or tree sometimes 30 feet high, bearing yellowish flowers in late spring. Native of Europe.

CUCURBITACEAE

These are annual or perennial succulent herbs, usually trailing or climbing by means of tendrils; about 700 species in 90 genera; mostly of tropical regions around the world, but some species extending into temperate zones.

IBERVILLEA LINDHEIMERI (Gray) Greene. fig. 9. Grains, when expanded, approximately spherical, about 59μ in diameter, tricolpate with furrows long and tapering to somewhat rounded ends. Exine thick, finely reticulate pitted.

Slender climbing or trailing herbs. In valleys, Tex. to so. Calif. Spring to fall. The genus comprises about 8 species of perennial vines in Mexico and southern U. S. A.

LUFFA ACUTANGULA Roxb. (*L. foetida* Cav.). Grains spheroidal, about 86μ in diameter, tricolpate with medium-long tapering furrows; furrow membranes flecked with a central streak of granules. Pores rather small, circular or elliptical in outline with their major axis directed meridionally. Exine apparently covered with fine bristles, in this respect bearing some resemblance to that of *Cucurbita*.

A strong vine, in cultivation in America and escaped in tropical America. The genus comprises 7 or 8 species, native of the Old World tropics.

CUCURBITA PEPO L. (type). Grains uniform, spherical, 130–145μ in diameter, without furrows but with about 10 large circular pores, 20–27μ in diameter. Each pore is provided with an operculum adorned with numerous short bristles and one or two long sharp spines, resembling a spiked helmet. The arrangement of the pores over the surface of the grain is not isometric, but approaches the tasithynic, suggesting that the pores represent reduced furrows. Intine rather thick and rigid. Exine covered with closely packed bristles giving it a granular appearance, also provided with many large sharp spines. With the highest magnification these are seen to be uniform shafts of homogeneous material, standing at right angles to the surface, about 6.5μ long, sharply pointed at their summits and flaring at their bases but approximately cylindrical through their central part. They are beautifully symmetrical in their arrangement which is almost exactly isometric.

The species exists in cultivation in many varieties, including such forms as the bush pumpkin, summer squash and yellow-flowered gourds. The genus includes about 10 species of annual or perennial trailing herbs, probably all American.

LAGENARIA LEUCANTHA Rusby (*L. vulgaris* Ser.). Grains in general form similar to the type, 160–190μ in diameter. Germ pores 9–12 in number and 30–

35μ in diameter. Spines of the exine 6.5μ long, but narrowed at the base instead of flaring as in the type. Surface of the exine appears to be finely granular, but may be composed of tightly packed bristles as in the type.

The genus contains but a single species, a variable long-running annual; native of the Old World tropics, but now wide-spread in warm countries, and in cultivation represented by many varieties such as the dipper and calabash gourds.

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Explanation of plates

All figures were drawn from studies made at a magnification of 900, using a Zeiss 3 mm. apochromat objective, N.A. 1.4, and paired 15×binocular eye pieces. Measurements, except those of very large grains, were made at a magnification of 1800, using 2 mm apochromat objective, N.A. 1.3, and a 20×eye piece. The sizes of the drawings are chosen to best display the characters of the grains and do not bear a constant relation to their sizes. The measurements given are those of average dimensions.

PLATE 20

Fig. 13. Pollen grain of *Sparganium androcladum*, about 23μ in diameter, showing its coarsely reticulate surface and single germ pore.

Fig. 14. Pollen grain of *Heliconia Bihai*, about 80μ in diameter, showing the thin transparent exine bearing numerous warts, and the thick transparent intine surrounding the cell contents, the darkened central globe.

Fig. 15. A single spine from a grain of *Laurus nobilis*. These are slightly larger than those of *Benzoin* (q.v., fig. 29, Pl. 22), otherwise exactly the same.

Fig. 16. Pollen grain of *Comptonia peregrina*, about 27μ in diameter, with three pores, seen in side view.

Fig. 17. Pollen grain of *Pontederia cordata*, about 48μ in length, side view showing one of its two furrows; the other furrow is exactly opposite. The dorsal surface is towards the left and is connected with the ventral surface, towards the right, by two narrow isthmuses, one at each end of the grain (cf. fig. 8).

Fig. 18. Pollen grain of *Sedum acre*, about 17$\times$16μ, side view.

Fig. 19. Pollen grain of *Brasenia Schreberi*, about 57μ in length, side view, showing its single asymmetrical furrow.

Fig. 20. Pollen grain of *Sedum acre*, polar view, cf. fig. 18.

PLATE 21

Fig. 21. Pollen grain of *Banksia Candolleana*, about 51$\times$24μ. Its two germ pores are seen one at each end of the grain.

Fig. 22. Pollen grain of *Ternstroemia granulata*, about 17μ in diameter, side view.

Fig. 23. Pollen grain of *Sterculia apetala*, about 30$\times$33μ, side view.

Fig. 24. Pollen grain of *Aralia spinosa*, about 30μ in diameter, polar view.

Fig. 25. Pollen grain of *Eucalyptus diversicolor*, about 25$\times$19μ, polar view, showing its short pit-like furrows.

Fig. 26. Pollen grain of *Lomatia ilicifolia*, about 33μ broad, polar view, showing its triradiate flattened form and reticulate surface.

Fig. 27. Pollen grain of *Talisia depressa*, about 28μ in diameter, transverse optical section.

Fig. 28. Pollen grain of *Sambucus canadensis*, about 18μ in diameter, side view.

PLATE 22

Fig. 29. Pollen grain of *Benzoin aestivale*, about 33μ in diameter, showing its thin transparent exine bearing numerous conical sharp spines, and thick transparent intine.

Fig. 30. Pollen grain of *Gaudichaudia Schiediana*, about 55μ in diameter. A triradiate center of convergence of furrows is uppermost and slightly to the right. There is another such triradiate center on the opposite side but with its furrows alternating with those of the upper center. Altogether there are 12 furrows.

Fig. 31. Pollen grain of *Sapindus marginatus*, about 18μ in diameter, polar view.

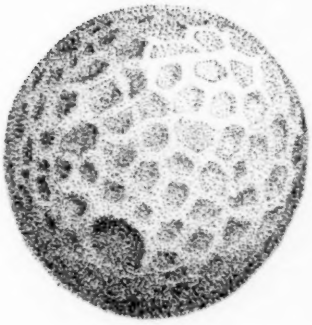
Fig. 32. Pollen grain of *Celastrus scandens*, about 23μ in diameter, polar view.

Fig. 33. Pollen grain of *Ailanthus glandulosa*, about 26μ in diameter, polar view.

Fig. 34. Pollen grain of *Parthenocissus hirsuta*, about 30$\times$40μ, side view.

Fig. 35. Pollen grain of *Zizyphus Jujuba*, about 22.5μ in diameter, polar view showing the three furrows which are merely slight depressions in the exine.

Fig. 36. Pollen grain of *Rhus glabra*, about 37μ in diameter, side view.



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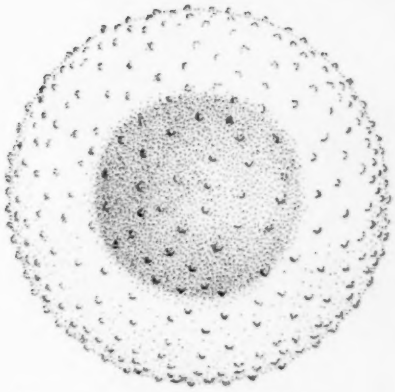

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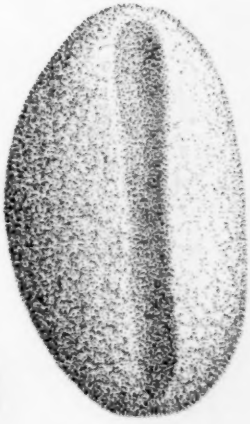

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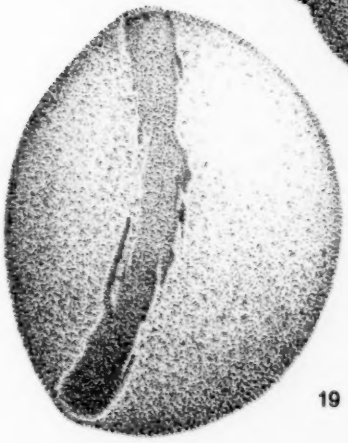

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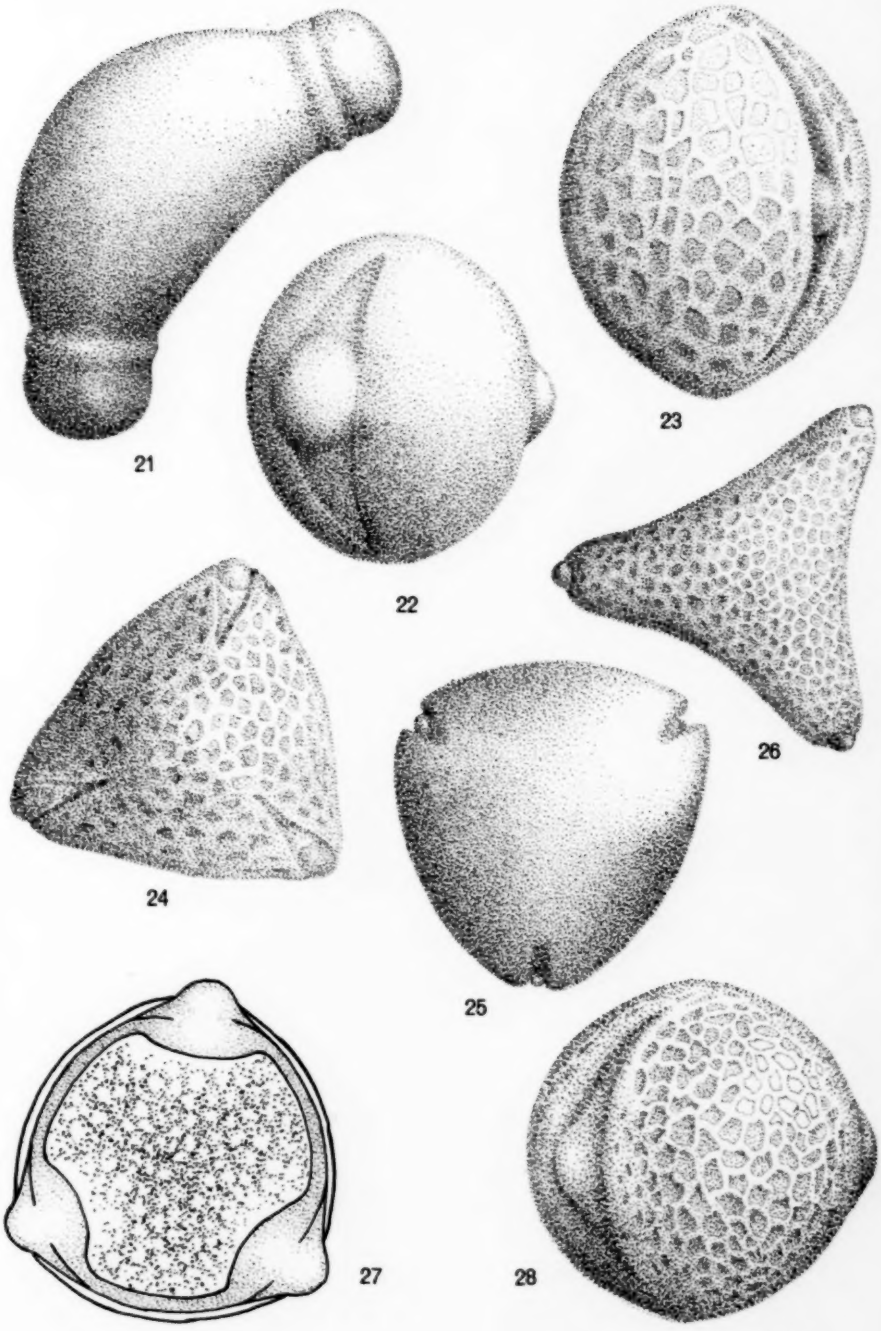

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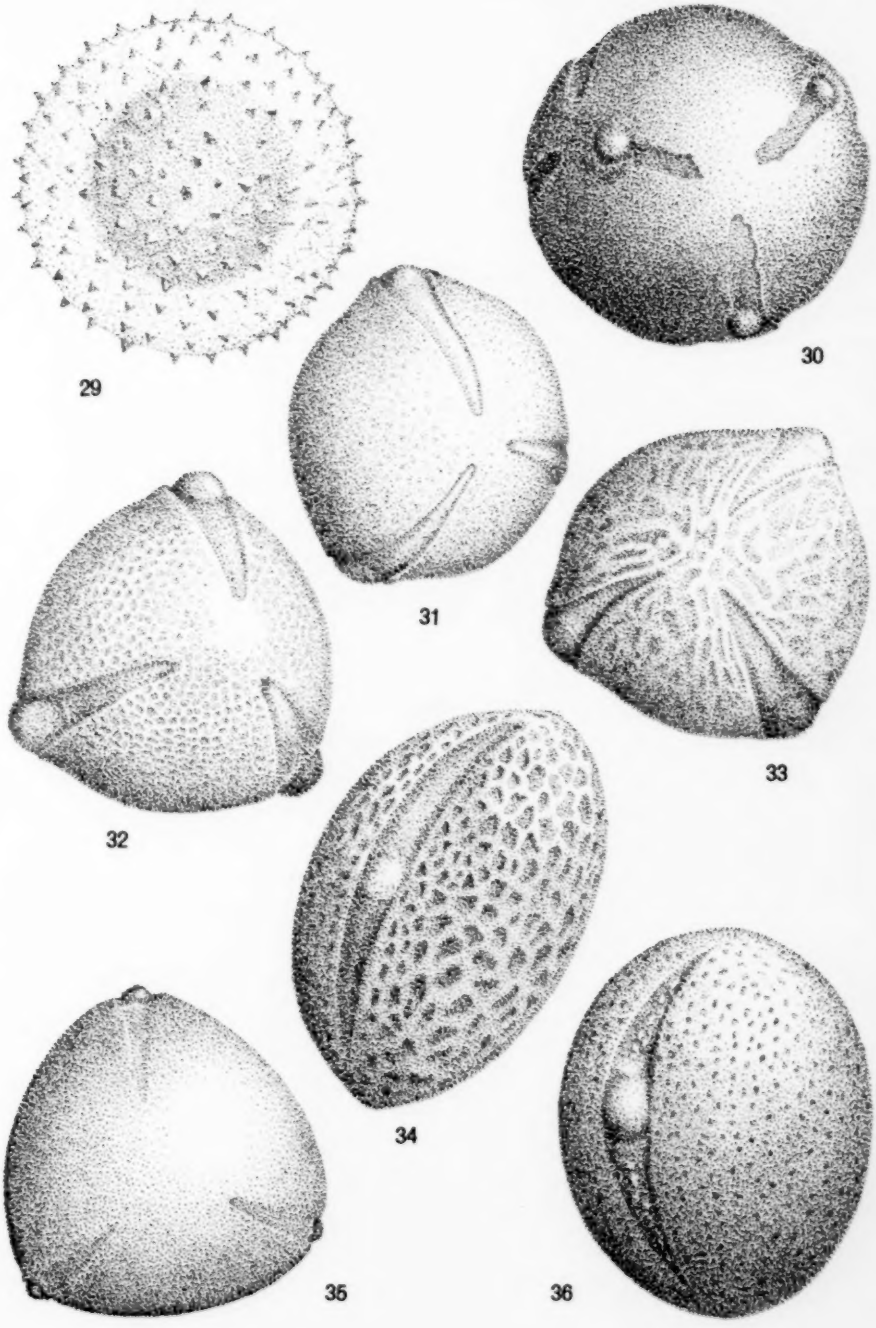

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An hermaphroditic self-sterile but cross-fertile condition in Pleurage anserina[1]

L. M. Ames

(with one text figure)

Much thought has been given to the sexuality of the fungi in late years. The discovery of heterothallism in the Mucorales by Blakeslee, and subsequently in the Ascomycetes, Eubasidiomycetes, rusts and smuts by other investigators, has stimulated intensive interest in this subject which at the present time is receiving great attention especially in the rusts and in the Ascomycetes. The present interest concerning this condition in the fungi goes back to the pioneer work of Blakeslee who obtained experimental evidence for heterothallism in the Mucorales by isolating and growing single spore cultures which by themselves produced only asexual spores, but which when certain of them were mated together produced rows of zygospores along the lines of intermingling hyphae. On this basis (Blakeslee, A. F. 1904. Sexual reproduction in the Mucorineae. Proc. Am. Acad. Arts and Sci. **40:** 205–319. *pl. 1–4*) he interpreted heterothallism in relation to sex as follows: "The assumption that their differentiation to (+) and (−) strains was indicative of a corresponding sexual difference, and that the strains thus designated should be regarded respectively as male and female, or vice versa, although naturally suggested by the observed condition, did not at first appear to be warranted. Evidence, however is not lacking which would seem to justify such a conclusion." With this evidence and with additional data Blakeslee established the fact that in certain of the Mucorales heterothallism involved the fact that there was present in one mycelium the potentiality of only one sex. Because heterothallism involving uni-sexuality was thus established in certain cases in the Mucorales, it has become the generally accepted view that heterothallism and uni-sexuality in the fungi are synonymous terms. Although this assumption has been found to be an adequate explanation for the sexual condition in certain species of fungi, it seems natural to suppose that other conditions may exist.

The writer working with *Pleurage anserina* (Ces.) Kuntze has found a sexual condition which modifies the conception of sexuality as outlined above, and offers a different interpretation of the sexual condition in this fungus. Previously the writer (Ames, L. M. 1930. A study of some homothallic and heterothallic Ascomycetes. Mycologia **22:** 318–322) had reported a homothallic condition in this fungus as the result of work done with single spore cultures from normal bi-nucleate ascospores which occur four in an ascus. At that time, also, the writer had observed that occasional

[1] Contribution from the Cryptogamic Laboratory of Harvard University No. CXI.

asci contained either more or less than the normal number of spores, for example now and then asci contained three normal bi-nucleate spores and two small uni-nucleate spores. At that time, however, the sexuality of the small uni-nucleate spores was not determined.

Meanwhile E. Silver Dowding (Dowding, E. Silver. 1931. The sexuality of the normal, giant, and dwarf spores of *Pleurage anserina* (Ces.) Kuntze. Ann. Bot. **45**: 1–15. *pl. 1+f. 1–10.*) reported that mycelia derived from dwarf uni-nucleate spores of *Pleurage anserina* were heterothallic, and in the same article she pointed out also that the mycelium from the normal ascospore bore no kind of secondary spore, stating: "The mycelia bore neither oidia nor any other kind of secondary spore which might be a source of contamination of the cultures."

During the fall of 1930, however, the writer while working on cultures derived from these small uni-nucleate spores of *Pleurage anserina* and studying the compatibility of strains derived from these uni-nucleate spores by pairing them in all possible combinations, discovered that in addition to the coiled ascogonia (see text fig. 1), from which the perithecial fundaments develop, there were produced on short branches of the mycelium minute spherical spores (microspores) (see text fig. 1) which functioned as spermatia, and this involved a situation very different from that usually conceived of as heterothallism. Many single spore cultures were made and each was found to produce the two types of sex organs just mentioned. These cultures derived from single uni-nucleate spores, by themselves, never produce perithecia, even though both the ascogonia and spermatia are present and have every opportunity for self-fertilization because they are growing intermingled (see text fig. 1). However, when the mycelia of many single spore cultures are mated together in pairs in all possible combinations so that the spermatia of one have opportunity to fertilize the ascogonia of the other, it is found that approximately 50 per cent of such crosses produce perithecia, while in the other 50 per cent of the crosses the perithecial fundaments never complete their development. Subsequently, the writer using two strains found to be compatible, had no difficulty in artificially fertilizing the ascogonia of one with the spermatia transferred from the second, and the ascogonia of the second with the spermatia transferred from the first (see text fig. 1). Perithecia were developed in all cases only in the immediate area where the spermatia were placed.

In connection with these experiments on cross-fertilization it was noted that the spermatia never produced mycelia nor germinated on nutrient substrata. Spermatia, under observation both in Van Tieghem cells and on several different types of nutrient agar, swelled several times in volume,

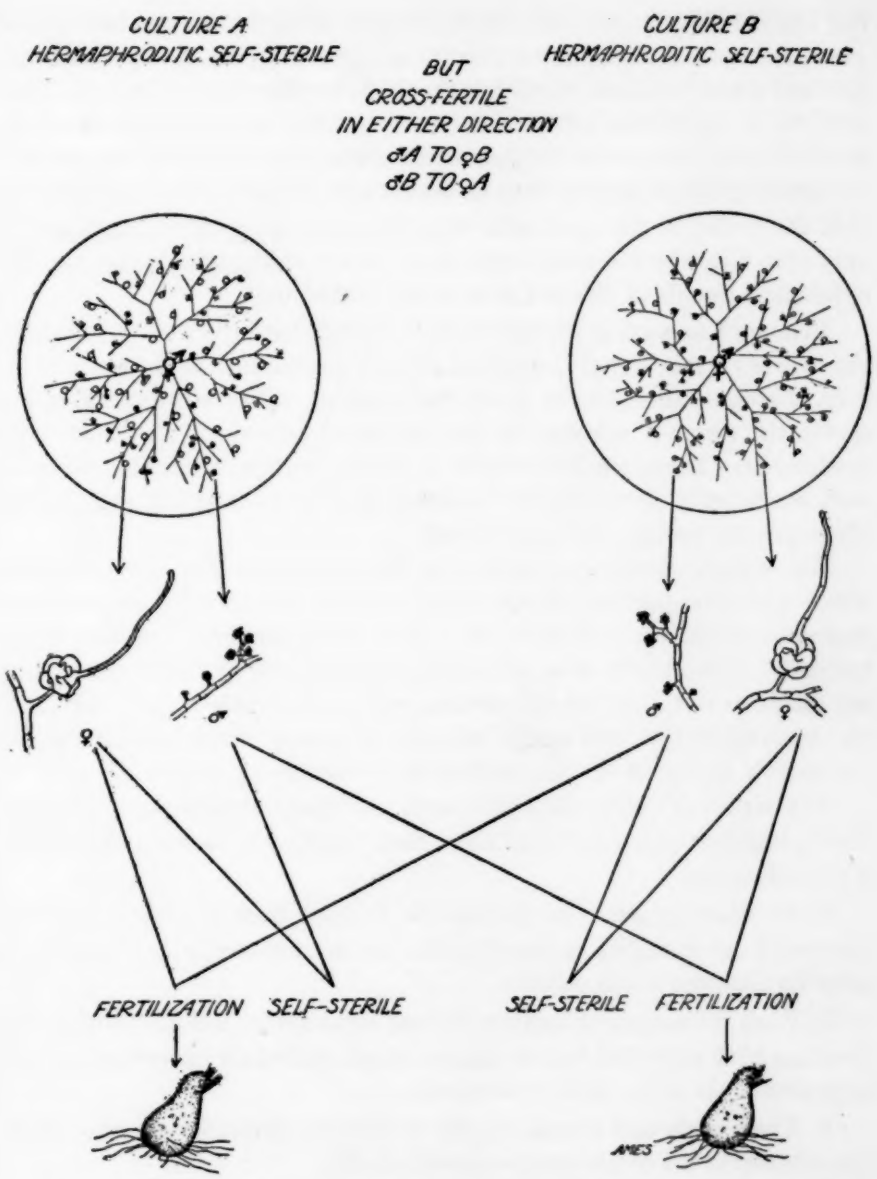

Fig. 1. Diagrammatic representation of the sexual condition in the hermaphroditic self-sterile strains derived from the uni-nucleate ascospores of *Pleurage anserina*, and of the production of perithecia by cross-fertilization of compatible strains. The young ascogonia are drawn from a photomicrograph and are in proportion to the size of the spermatia.

but beyond their increase in size no further development has been noted even after several weeks under conditions apparently suitable for germination and under the same conditions in which fertilization took place. However, when spermatia are placed on compatible ascogonia the development of these into perithecial fundaments was discerned with the unaided eye even within as short a time as seventy-two hours. This fact indicates that the nuclei of the spermatia enter the trichogyne of the ascogonium very soon after the spermatia come in contact with the trichogyne, and the cytological details of this are now being worked out.

Inasmuch as some investigators have found that injury to mycelium in the case of certain Fungi Imperfecti induces sporulation at the place of injury, it seemed necessary to prove that possible injury in transferring the spermatia was not responsible for the development of the perithecial fundaments. Therefore lacerations of the mycelium of similar cultures were made with sterile transfer needles, and in no case did such injury stimulate any perithecial development.

The writer, therefore, is driven to the conclusion that the ascogonia, which are abundant on all of these cultures from single, uni-nucleate spores, develop into perithecia only after being fertilized by compatible spermatia. The strains from uni-nucleate ascospores of *Pleurage anserina* are therefore not heterothallic strains, male and female respectively, but are hermaphroditic self-sterile strains, requiring cross-fertilization by compatible opposites for the production of mature perithecia.

The writer is continuing this work and from observations recorded above, together with additional data, feels justified in drawing the following conclusions:

1. In *Pleurage anserina* the mycelia derived from small uni-nucleate ascospores are in reality hermaphroditic strains, self-sterile, but capable of cross-fertilization if compatible.

2. Each monosporous culture derived from dwarf, uni-nucleate spores develops both male and female organs; small spermatia (microspores) and large ascogonia with coiled trichogynes.

3. These male and female organs on mycelia derived from monosporous cultures of the dwarf spores are self-sterile.

4. Cross-fertilization by transferring compatible spermatia from one culture to another results in the formation of mature perithecia from the ascogonia thus fertilized.

5. Injury to the mycelium by sterile transfer needles does not stimulate the production of perithecia.

6. The non-production of mycelium from the spermatia together with

their effect in cross-fertilization indicates that they do not function as conidia, but as true spermatia.

7. Between compatible single spore strains successful cross-fertilization of the ascogonia of one with the spermatia transferred from the second, and the ascogonia of the second with the spermatia transferred from the first, demonstrates that the male and female organs are each functional.

Laboratories of Cryptogamic Botany
Harvard University

The non-sexual and the sexual functions of microconidia of Neurospora

B. O. Dodge

(WITH PLATES 23, 24 AND ONE TEXT FIGURE)

I have previously[1] reported that certain albinistic strains of *Neurospora sitophila* produce microspores of the type formed by *Botrytis* and *Sclerotinia* as figured by Woronin. These microconidia germinate to produce mycelia which appear to differ in no way from mycelia derived directly from ascospores or from monilioid conidia. Furthermore, races 56.2 and 56.6, which are of opposite sex in their reactions[2] both produce such microspores. It was stated in the paper referred to that the mycelia derived from these races could be mated to produce perithecia. I have been reminded, however, that it was not stated that these mycelia could be *mated together*. This opportunity is taken to make this point clear as requested, and to report some further work along the same line. As a check on my own culture work, I have asked my assistant, Miss Marjorie E. Swift, who has acquired an excellent technique for isolating very small spores through her work on *Penicillium* and other fungi, to repeat my work on microconidia. Much additional evidence supporting certain statements included here resulted from her careful work.

Humphrey[3] states that microconidia of *Sclerotinia fructigena* of the Woronin type germinated in his cultures and produced normal mycelia. His descriptions of the process and the accompanying figures are rather convincing even though others have questioned his work. My own one attempt to obtain germination with microspores of *S. fructigena* also resulted in failure.

Brierley[4] has reported (he has in a recent letter positively confirmed that report) that microconidia of *Botrytis cinerea* germinate freely to pro-

[1] Dodge, B. O. Breeding albinistic strains of the *Monilia* bread mold. Mycologia **22**: 9–38. 1930.

[2] Is it necessary to explain again that I always use the terms "sex" and "opposite sex" simply for convenience until someone tells us just what it is that sets off the mechanism which regulates perithecium formation. A good term for this condition is needed. To quote from one of my other papers[11]: "In this paper the terms hermaphroditic, homothallic, haplomonoecious and bisexual are all used in the same sense to indicate a mycelium having two kinds of nuclei as to their sex, *or whatever it is here that corresponds to sex.*"

[3] Humphrey, J. E. On *Monilia fructigena*. Bot. Gaz. **18**: 85–93. 1893.

[4] Brierley, W. B. The microconidia of *Botrytis cinerea*. Kew Bull. Misc. Information **1918**: 129–146. *pl. 5*. 1918.

duce normal *Botrytis* mycelia. There can be no doubt, from his account of the way these microspores are formed, that they are entirely different from the ordinary conidia which characterize the genus *Botrytis*. Are they morphologically spermatia, homologous with the microconidia of *Sclerotinia* as figured by Woronin? Whether these little bodies germinate or not, the germination test will be the basis for the conclusions which will be reached by those who hold that *function* determines homologies.

The microconidia of *Neurospora* are, as stated in the paper referred to[1], apparently formed in much the same way that they are in *Botrytis* and *Sclerotinia*, except that instead of arising on bottle-shaped "sterigmata" they form directly from individual cells of the branched microsporophore. (In several species of *Sclerotinia* microspores also arise in much the same way directly as buds on the surface of the macroconidia and ascospores as well as from the cells of germ tube hyphae without evident sterigmata.) They are not formed internally as endospores, yet they appear as though forced out through a collared opening, one after another, occasionally adhering in a little chain for a short time. This collar structure may, however, represent a very short sterigma. The illustrations (text fig. 1, a-f) show about what one sees under oil immersion magnification. Figure 1, g, is taken from Brierley's paper on *Botrytis* for comparison. Plate 23, a, b, shows the branched microconidiophores, under various magnifications. Professor R. A. Harper, and others who were kind enough to examine my preparations, were satisfied that these structures are true microconidia and not small monilioid conidia. They are to be compared with the microconidia of *Sclerotinia*. At c (plate 23) are seen numbers of microconidia at the time they were sowed for germination, and at d, equally magnified, a few of the same bodies about 40 hours later, when some of them had germinated. They always do germinate on corn meal agar if given two or three days to do so. It is necessary to exclude all monilioid conidia and mycelial fragments, otherwise the plate will be overgrown before the microspores have a chance to germinate.

When one accidently sows an old detached microsporophore along with the microspores it does not sprout out as would an ordinary mycelial branch. It lies on the surface of the agar unchanged for a long time (for at least 80 hours as was observed in one case). In the meantime microspores all around it will have germinated and grown out branched systems of hyphae. Of course if it is still attached to its parent hypha, the hyphal cells may sprout within a few hours and ruin the experiment. It may be that even the old cells of the microsporophore would eventually send out hyphal branches if left long enough, particularly if one that had produced only a few microspores were tried out. If the microspore is still attached

it will germinate and give the appearance of a cell sprouting. There is no reason, except complete differentiation, why a young microsporophore branch should not sprout out vegetatively. After the whole crop of microspores has been produced, that would naturally leave the individual cells exhausted. These microsporophores and the little "spores" which they produce are certainly curious structures. I shall show later on that the microspore can perform another function which supports the theory that in their morphology they represent ancestral male elements. When they germinate as described above, however, they are simply reverting to perform a vegetative function.

The production of microspores is not confined to the non-conidial albinistic races. Race Arl.10.42 which produces monilioid conidia, also

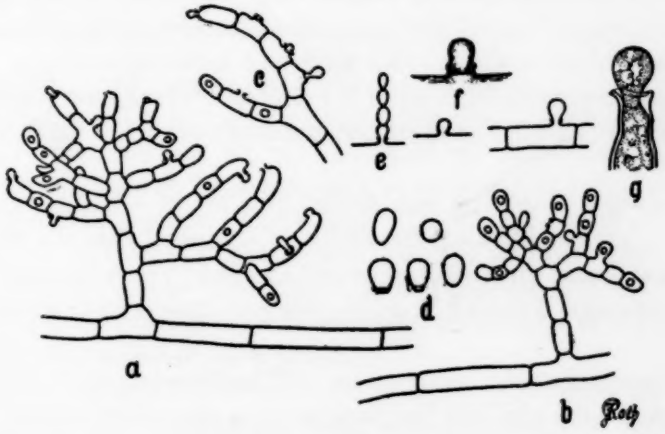

Fig. 1, a–f. Origin of microconidia in *Neurospora sitophila*. Various magnifications. The little circle in a cell is to represent a surface view of the collar-like projection from which microspores arise. Several cells show a side view of this collar. g. Sterigma and microconidium of *Botrytis cinerea*, after Brierley.

forms microconidia. Strains S_1 and S_6, of *N. tetrasperma* produce both kinds of conidia. Furthermore, certain normal conidial races of *N. crassa* which were examined in plate cultures, were found to be producing microspores rather abundantly. The photographs (plate 23, e-g) show that the microconidiophore may be either unbranched (e) or, even dichotomously branched (g). At f, lower center, are seen two microspores as they arise from adjacent cells. Microspores of *N. crassa* are usually ovoid to pear-shaped, and slightly brownish in color. They are formed just as they are in *N. sitophila* and *N. tetrasperma*, and germinate in the same slow way. Mycelia from microspores derived from pure conidial races produce monilioid conidia and microconidia in turn.

MATING MYCELIA DERIVED FROM MICROSPORES

Starting with the non-conidial races 56.2 and 56.6, which are haplonts A and B, and of opposite sex in their reactions, a number of single-microspore cultures were isolated. Some 20 matings of these cultures resulted in an abundance of mature perithecia in each case (plate 24, e). When the first set of single-microspore cultures had produced microspores in turn, a second generation set of cultures was obtained. Again twenty matings were made between pairs of mycelia obtained from the second generation of microspores. In every case, again, an abundance of perithecia matured. This confirms fully the assertion[1] that these microspores germinate like true spores and their mycelia are perfectly normal, showing the same type of sexual reaction as that of the parent mycelia from which the microspores were obtained. Because of their very small size they are probably, in general, uninucleate. This gives us a better opportunity to study such somatic segregations as occur in cultures. Ordinary monilioid conidia contain several nuclei, and therefore mutations are more likely to escape notice.

Another line of cultures was started from strain Arl.10.42, which also produces a few monilioid condia, and it so happened that the microspore isolates in this case turned out to be non-conidial[5]. The microspore isolates from a good conidial race of *N. crassa*, however, produced an abundance of conidia.

The theory that the ascomycetes and basidiomycetes have been derived from the red alga line has been much strengthened within the past few years. Professor R. A. Harper in reviewing Rosenvinge's work on *Phyllophora brodiaei*[6] before a group of botanists recently, pointed out how perfectly this alga parallels a typical ascomycete in its morphological features. Unintentionally, because he does not even mention the fungi, Svedelius[7], in his discussion of lines of evolution within the red alga group, has made it easier for mycologists to see how these algae and the ascomycetes are very similar in their organization.

[5] Strain Arl. 10 is the unstable parent strain (see reference in footnote no. 1) from which, by plating out the monilioid conidia one can obtain races such as Arl. 10.42 which produce very few monilioid conidia. When I refer to a race as non-conidial it is meant that it produces no monilioid conidia. It may or it may not produce microconidia in any particular culture.

[6] Rosenvinge, L. K. *Phyllophora brodiaei* and *Actinococcus subcutaneus*. Det. Kgl. Danske Videnskab. Selskab. Biol. Middelelser. VIII. **4**: 1–40. 1929.

[7] Svedelius, N. Nuclear phases and alternation of generation in the Rhodophyceae. Beih. Bot. Centralb. **48**: 38–59. 1931.

Very recently it was my privilege to read in advance of publication a preliminary paper by F. L. Drayton[8] on "The sexual function of the microconidia in certain discomycetes." He reports that in *Sclerotium Gladioli* the microconidia function the same as do the "pycniospores" of the rusts; that is, he "spermatizes" certain receptive structures with non-germinating microconidia of his *Sclerotium*, with the result that apothecia of the genus *Sclerotinia* are developed in his culture. He would argue on this basis that microconidia are male in their morphology and function, and that: "It is highly probable that this sexual mechanism is operative, with perhaps slight modifications in all spermatia-producing Ascomycetes . . . ." This would certainly be the very best kind of evidence that the red algae were the ancestors of our higher ascomycetes.

"SPERMATIZING" WITH MONILIOID CONIDIA (N. TETRASPERMA)

Unreported experiments demonstrated before a group of university students a few years ago may be of interest in this connection. Race S_1 (*N. tetrasperma*, haplont B) was grown in one petri dish and race S_6 (haplont A) in another for a few days, or until the mycelia had covered the plates. The monilioid conidia from S_1 were then sowed in a drop of water on two or three different spots on plate S_6, and vice versa. The drop of water is quickly absorbed by the agar and disappears. A few days later perithecia were formed over small areas where the drops of water carrying the monilioid spores had been placed.

This experiment has been repeated recently. The results show beautifully how one can "spermatize" with ordinary monilioid conidia. Plate 24, f, (the two upper spots), shows such a result from "spermatizing" with ordinary conidia. The two lower spots will be referred to in another connection.

It will, of course, be said that when these conidia are laid on a spot in a drop of water, they germinate quickly and produce mycelia which react in the same way that any two mycelia of "opposite sex" react, whatever way that may be, to produce perithecia in a culture. Evidence that this is probably not the case is furnished by an interesting experiment. A plate was inoculated with race S_6 on one side, and another plate was inoculated in the same way with race S_1. After the mycelia had grown part way across the plates in each case, monilioid conidia from S_1 were placed on a marked spot at the tip ends of hyphae in plate S_6, and monilioid conidia from S_6 were placed in a similar position in plate S_1. The plates were then incubated

[8] Drayton, F. L. The sexual function of the microconidia in certain discomycetes. Mycologia **24**: 345–348. 1932.

for four days. During this brief period perithecia had begun to develop rapidly on the marked spot in plate S_1, and the original mycelium in the plate had grown out to the edge of the culture. This is an illustration of successful spermatization with macroconidia. (For a similar picture see Plate 24, c.)

Quite a different picture was presented in the other culture (Plate 24, a). What had happened is easily understood, and it throws much light on the question as to just what is going on in both cases. S_6 race is a rather slow-growing race, so that the conidia of S_1, being in contact with fresh agar medium at the tips of the S_6 hyphae, germinated normally and grew out rapidly in the only direction not already occupied by the oncoming hyphae of race S_6, that is, away from the hyphal tips. Spermatization could not occur because the conidia had already germinated to form hyphae. One could see on the second day how the S_1 hyphae were spreading out in a broad fan-like growth, always keeping out beyond and around the more slowly growing S_6. The photograph shown in Plate 24, a, gives the picture seven days after the conidia from race S_1 had been placed on the spot marked by the circle at x. The curved line marks the limit of hyphal growth at the time spermatization was attempted. The culture in which spermatization of S_1 by monilioid conidia from S_6 was successful presented a picture like that shown at c in Plate 24, although this is a picture of another culture to be described later. One can successfully spermatize a culture of race S_6 with conidia from race S_1 if he places the conidia on the mycelium back of the hyphal tips, or say, at y (see Plate 24, a) instead of at x as was actually done in the experiment. This has been done several times and perithecia usually appear on the marked spot within 48 hours if the culture is not an old one. The experiment in which macroconidia were placed on mycelia of the opposite sex as described here was originally suggested by another of somewhat different nature.

Races S_1 and S_6 were grown in separate plates as before. After about ten days a small block of agar from S_1 now covered with hyphal growth etc. was put in plate S_6, and vice versa. The results were quite different, though perithecia were formed in both cases. Where the block of S_6 agar was laid on S_1 plate, the perithecia were formed on the S_6 block and not on the agar in the S_1 plate. Where the block of S_1 was laid on plate S_6 the fruit bodies were formed on the S_6 agar in the plate, not only directly under the little S_1 block but for some distance away on all sides. This behavior may not hold in all cases, but here, at least, it looked as though the S_1 were the more potent spermatizing or diplodizing agent. This is quite the opposite of the conclusion one reaches when he observes the results obtained in the experiments on spermatizing the microconidia described below.

"SPERMATIZING" WITH MICROCONIDIA (N. TETRASPERMA)

The experiment on "spermatizing" noted above was repeated recently but microconidia instead of monilioid conidia were used. At the same time the experiment was checked by using monilioid conidia for "spermatizing" at other points. Strains S_1 and S_6 were grown as before in separate petri dish cultures. After three days, or when the mycelia had covered the plates, microspores were taken from S_6 and placed in drops of water on marked spots on plate S_1. At the same time macroconidia in drops of water were placed on other marked spots on the same plate. Four days later perithecia had begun to develop in all cases, not only where the microconidia were used for spermatization, but also where the monilioid conidia were used. Plate cultures of S_6 were also successfully spermatized with macroconidia from S_1, but microspores of the latter were not available at the time.

There are two conditions that bear on the success of these experiments. First, the mycelium to be spermatized should not be too old. Several attempts to stimulate perithecium formation in cultures two weeks old resulted in failure. Second, in order to spermatize successfully the microspores should be obtained from fairly fresh cultures, cultures only a few days old. Microspores from cultures 25 days old, on the other hand, germinated well when sowed on sterile agar plates. This would seem to indicate that although age may be an inhibiting factor in spermatizing, germination of the microspores is not seriously affected. Further work along this line is desirable.

"SPERMATIZING" WITH MICROCONIDIA AND MONILIOID CONIDIA (N. SITOPHILA)

Albinistic non-conidial races 56.6 and 56.2 were grown separately three days in plate cultures. Microconidia from the 56.6 line were used to spermatize plate 56.2 at certain marked spots, and microconidia from the 56.2 line were used to spermatize plate 56.6 at certain spots. As a check and for comparison monilioid conidia from the normal conidial race 56.3 were used to spermatize plate 56.6, and monilioid conidia from race 56.8 were used to spermatize plate 56.2 at certain marked spots. The plates were then incubated at about 25°C. for only forty-eight hours when perithecia began to show on each of the marked spots in every case except where the microspores from line 56.6 had been placed on plate 56.2. Perithecia developed on these spots also, however, hours later (Plate 24, b). Since under similar conditions the microspores, if placed on corn meal agar and incubated, would have just begun to germinate after forty-eight hours, we may assume that at least the microsopores actually functioned as spermatia, passing their nuclei on to whatever receptive organs are involved.

The macroconidia of *Neurospora sitophila* seem to function equally well as "spermatizing" agents, just as was proved to be the case in *N. tetrasperma*. Each of two agar plates was inoculated on one side with the non-conidial race 56.6. After forty-eight hours the mycelium had grown about half way across the plate in each case. A line was drawn on the bottom of the plate to mark the limits of growth. Macroconidia from race 56.3 were placed on a marked spot in one plate so that some of the conidia were in contact with the hyphal tips. Microconidia from race 56.2 were placed in like manner on the other plate. The cultures then incubated for forty-eight hours. By the end of this time the original mycelia had overgrown both plates and perithecia were already showing in both cultures but only on the marked spots which had been spermatized (Plate 24, c, d). No doubt perithecia could have been detected several hours earlier had the cultures been examined. When 56.2 is spermatized either with microspores from race 56.6 or with macroconidia from race 56.8 it requires a longer time for perithecia to develop, and there are, for some reason, not so many of them.

One can reverse the experiments described above by growing conidial races in plate cultures for a day or two and then spermatizing with microspores on some spots, and with macroconidia on other spots. For example, when conidial race 56.3 was spermatized with microspores of 56.6, and on other spots with macroconidia of race 56.8 many perithecia developed after about sixty-four hours. Cultures of conidial race 56.8 were spermatized in like manner with microspores of race 56.2 and on different spots with macroconidia of race 56.3. Perithecia were plentiful on all of the spermatized spots in this case also at the end of sixty-four hours. When mycelia of these conidial races of opposite sex reaction are grown together in tube cultures it usually requires five or six days before perithecia begin to show.

SEXUAL VERSUS NON-SEXUAL FUNCTIONS

Holding that the theory of origin of the ascomycetes from the red algae is the more plausible one, it must be conceded that there was no doubt as to the facts in the case when reporting phenomena[1] (germination of microconidia) that may well be interpreted to support the opposing theory, namely, that the ascomycetes have arisen in a monophyletic line from the oomycetes. Now, Drayton says that his microconidia function the same as do the "pycniospores" of the rusts, and adds that the few cases where germination of microconidia of ascomycetes is reported, remain to be satisfactorily explained. Just how do the "pycniospores" of the rusts function? Some say they germinate, but Andrus[9] alone, of those who

[9] Andrus, C. F. The mechanism of sex in *Uromyces appendiculatus* and *U. vignae*. Jour. Agr. Res. 42: 559–589. 1931.

have been studying this question recently, says positively that they do not germinate. They are true spermatia, he says, and function as such by passing their nuclei on to trichogynes or trichogynous hyphae. Whatever may be the way the pycniospores of the rusts and the microconidia of *Sclerotium Gladioli* function, we do know that when microspores of *Neurospora* germinate to form mycelia, which, when properly chosen, can be *mated together* to produce perithecia, they are not functioning solely as male organs or spermatia. They are functioning as true spores. One can claim however, that they actually perform their spermatium function when afforded an opportunity to provide the impulse for perithecium formation, that is, when one "spermatizes" with them. The zoosporangia of certain species of the Peronosporales under particular conditions of moisture and temperature germinate like ordinary conidia to produce infection tubes. Zoospores of *Synchytrium* can reinfect the host directly, or they can function as gametes and fuse in pairs, male with female, but often showing merely relative sexuality, as in case of *Ectocarpus*.

There is a very intriguing theory which was briefly stated by Kniep[10]. A rust like *Puccinia Helianthi* is in fact hermaphroditic or haplo-monoecious, and not heterothallic. Each mycelium produces male elements, spermatia, and also something else that functions as a female element. We are misled into thinking that it is heterothallic because it is necessary to cross-spermatize to obtain aecia. Kniep says this may be nothing but a form of self-sterility determined by factors which segregate according to the mono-hybrid scheme. Had he known at the time that each mycelium of *Neurospora* also produces microspores in addition to ascogonial coils and sterile perithecial bodies, he would, no doubt, have applied the same line of reasoning to account for the results to be obtained by mating pairs of mycelia each of which is by itself sterile. (In one of my earlier papers[12] it was stated that: "Mycelia of species of *Neurospora* produce coiled structures which very likely are morphologically sex organs. . . . The two mycelia which are opposite in their reaction in the production of perithecia have been classified provisionally as haplonts A and B.") Gwynne-Vaughan and Williamson[13] have since reported that all races of heterothal-

[10] Kniep, H. Die Sexualität der niederen Pflanzen. Jena. 1928. See pp. 454, 455.

[11] Dodge, B. O. Inheritance of the albinistic non-conidial characters in interspecific hybrids in *Neurospora*. Mycologia **23**: 1–50. 1931.

[12] Dodge, B. O. Production of fertile hybrids in the ascomycete *Neurospora*. Jour. Agr. Res. **36**: 1–14. 1928.

[13] Gwynne-Vaughan, H. C. I. & H. S. Williamson. Contributions to the study of *Humaria granulata*, Quel. Ann. Bot. **44**: 127–145. 1930.

lic *Humaria granulata* produce oogonia. Gregor[14] and Buisman[15], working independently, have reported on two species of *Ceratostomella* which are heterothallic, yet monospore cultures in all cases produce incipient perithecia and small asexual spores. *Sclerotium Gladioli* is still another example of the same sort, and Drayton[8] has, for the first time, in a convincing manner, demonstrated that the microspores can be made to function in "spermatizing" certain receptive organs to the end that apothecia are matured. Kniep points out[16] that one could assume with Correns in accounting for the reactions of our so-called heterothallic ascomycetes that each haploid mycelium contains potentialities of both male and female sexes, but that there are genes, "determinators," that impress on such a mycelium either a male or a female stamp when it comes to the origin of fruit bodies.

All of which is just another way of saying that the genes or factors that determine the primary sex function are not indissolubly linked with those factors regulating the development of ascogonial coils, perithecial frameworks, and spermatia (microspores). Or, to put it another way, a monospore mycelium of *Neurospora sitophila* is, to all intents and purposes, unisexual when it comes to sexual reproduction. As long as this gene or determinator does not weaken, that mycelium must react as, say, the male parent only. As yet the results of hundreds of tests have not brought to light any strain of *N. sitophila* derived from a single ascospore from an 8-spored ascus that would produce perithecia *with asci* without being mated in culture with some other strain. The discovery of such a strain is highly desirable, as it would serve to confirm Kniep's (Correns') theory for the rusts as applied to the ascomycetes like *Neurospora*. I am inclined to accept this theory in principle, in spite of the fact that the microspores in *Neurospora* can germinate and produce normal mycelia, because they can also be used to spermatize directly.

Why must the mycelium derived from a microspore be male, just because we may insist the microspore is homologous with the spermatium. In its sexual reaction the mycelium from a microspore or spermatium must be exactly like the mycelium that produced that microspore. The latter mycelium got all its elements of inheritance from a single ascospore nucleus. Segregation and distribution of genetic factors occurs just previous

[14] Gregor, M. J. F. A study of heterothallism in *Ceratostomella pluriannulata* Hedgcock. Ann. Myc. **33**: 1–9. 1932.

[15] Buisman, C. *Ceratostomella ulmi*, de geslachtelijke vorm van *Graphium ulmi* Schwarz. Tijdschr. Plantenz. **38**: 1–8. 1932.

[16] Kniep, H. Vererbungserscheinungen bei Pilzen. Bibliographia Genetica **5**: 371–478. 1929.

to ascospore formation at reduction, and not at "spermatogenesis," if we may refer to a microspore as a spermatium and the process of its formation as spermatogenesis.[17] A microconidium has, barring somatic segregation or mutation, all the potentialities of a monilioid conidium, all the potentialities of an ascospore, all of the potentialities of the whole mycelium for that matter. If you give a microspore the right cultural conditions there is no fundamental reason, except its small size, why it should not germinate. We naturally want to see the microspore pass on its nucleus without showing signs of germination to make it a good spermatium. In "spermatizing" with conidia it may be necessary for them to thin out the wall a little by going through the first stages of germ tube formation. If one grows S_1 mycelium of *N. tetrasperma* opposite S_6 in a petri dish culture[11], just to take one case for an example, it looks more as though the S_6 were being "diplodized," as Professor Buller would say, rather than spermatized, because the perithecia seem to be formed on the S_6 mycelium alone, the fruit bodies being placed more or less along the lines of mycelial growth of that haplont. According to the Correns-Kniep theory each mycelium of the pair is reacting as of one sex only. That is to say, as long as the "determinator" does not weaken, S_6 is the female parent only, here. This may possibly be true in the experiments with S_1 and S_6 previously described (p. 352) but it would not be easy to answer objectors who would insist, but without any proof, that, since one can spermatize equally well regardless of which mycelium of the pair furnishes the microspores, either mycelium, or both in the same culture, can act as the female parent.

No amount of speculation or theorizing on the nature of sex in the ascomycetes will alter the fact that one can breed and hybridize strains and species of *Neurospora* just as though he were dealing with unisexual races. If we leave out the idea of maleness and femaleness the old word

[17] In *Drosophila* spermatogenesis connotes or involves reduction division and segregation of certain genetic factors, whereas in *Neurospora* the formation of spermatia involves not segregation but only differentiation or coming to maturity. If one will cut off a young ascogonial coil of *Neurospora* and plant it in a culture medium, and if it buds at all, it will grow out into a normal mycelium which in turn will produce microspores as well as ascogonia. The reason why the microsporophores did not bud out to form mycelia in the experiments previously described was probably because they were not tried out until they were too old, or had become exhausted through the production of masses of microconidia. The development of antheridial branches as distinct from oogonial branches in *Pyronema* is a case of sex differentiation and not sex segregation. It is a coming to maturity of the mycelium. If one could cut off the antheridial branch very early in its growth it would no doubt bud out to form a normal mycelium which would produce both ascogonia as well as antheridia in turn. Whether any particular ascogonial or antheridal branch will become vegetative when excised will depend upon to what extent differentiation has already occurred.

heterothallism is still a good one, because the two mycelia that must be grown together to produce perithecia are different, although we do not know just how they are different. My results with *Neurospora* throw further light on the questions that might be raised with respect to the implications in my former papers,[18] namely, that self-perpetuating androgenetic, parthenogenetic, and syngamic (hermaphroditic) races exist in the blackberry rust.

Very interesting examples of the working out of incompatibilities were frequently encountered in the experiments on breeding interspecific hybrids previously described,[11] especially among the hermaphroditic hybrids. In the latter cases it was not difficult, by separating out the unisexual components, to prove that the incompatibility was quite aside from the question of sex. Whether sex as it works out in *Neurospora* is in the same category with sex of a pollen grain, a sperm, or an egg cell, may be a question. If it is not, it is a perfect substitute and it is regulated in the same way.

We have a four-spored species of *Neurospora* obtained from Dr. R. A. Toro in Porto Rico. It has behaved rather peculiarly. Single ascospore cultures produce perithecia abundantly, so that it is hermaphroditic, and it corresponds morphologically to *N. tetrasperma*. When the unisexual component strains of the Toro species were mated against S_1 and S_6, which are *N. tetrasperma* unisexual tester strains, no perithecia were formed in either case. Toro's species does not seem to hybridize readily with our *N. sitophila* and *N. crassa*, although in all these cases one can tell, by the reactions, when mycelia of opposite sex are being paired. This is an illustration either of interspecific sterilities or geographical incompatibilities. What species the Toro fungus really represents, is still an uncertainty. It behaves as though it were a different species altogether from the three we have in culture, even though morphologically it is like *N. tetrasperma*. By working out such forms as this we shall unquestionably arrive at a better understanding of what we mean by sex as well as what constitutes a species in these fungi.

After page proof of the above was received further data on the development of perithecia through spermatization have been obtained. In two plate cultures of *Neurospora sitophila*, strain 56.6, forty-eight hours old, "sclerotia" were visible only within about $1\frac{1}{2}$ centimeters from the original

[18] Dodge, B. O. Uninucleated aecidiospores in *Caeoma nitens* and associated phenomena. Jour. Agr. Res. **28**: 1045–1058. 1924; Cytological evidence bearing on the sexuality and origin of life cycles in the Uredineae. Proc. Internat. Congr. Plant Sci. **1926**: 1751–1766. 1929. Dodge, B. O. & L. O. Gaiser. The question of nuclear fusions in the blackberry rust, *Caeoma nitens*. Jour. Agr. Res. **32**: 1003–1024. 1926.

point of inoculation. The mycelium had grown practically across the plate in each case. Monilioid conidia of strain 56.3 were placed on a marked spot showing many sclerotia about half a centimeter from the inoculation point. A drop of water without conidia was placed on a corresponding spot in the other plate. Twenty-two hours later perithecia had begun to develop on the marked spot. None showed on the control. This provides further evidence that the monilioid conidia had functioned as spermatizers rather than as spores which germinated.

At the margin of growth where no sclerotia were visible at the time, monilioid conidia of 56.3 were placed in a marked area on one plate and check was provided by placing a drop of sterile water on a similar marked spot in the other plate. Twenty-seven hours later many perithecia began to show on the spermatized spot. Whether this difference of five hours represents the time required for the development of the necessary receptive structures is a question to be answered by later experiments.

On page 352 (Plate 24, a) an experiment was described showing the difference between the results obtained when macroconidia function as spermatizers and when they function normally as spores producing mycelia. This experiment has since been checked by using microspores instead of monilioid conidia. It has been shown that if the microspores are first allowed to germinate to produce small mycelia before coming in contact with a mycelium of the opposite sex, then the perithecia which are produced are distributed as they are in every case where two mycelia of opposite sex are grown in the same culture. That is, they are distributed progressively over wide portions of the plate, whereas if the microspores are placed directly on a mycelium of the opposite sex, then they act as spermatizers and the perithecia are confined largely to the spot over which the drop of water containing the spores spread at the time of spermatization.

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Explanation of plates

PLATE 23

a–d. *Neurospora sitophila;* e–g. *N. crassa.* Various magnifications.

a. Microconidiophores under low power; b. The central cluster from figure a; c. Microconidia just as sown on agar surface; d. Some of the same microspores about 40 hours later when germination was well under way, the same magnification as those shown in c; e. Unbranched microsporophore showing two little chains of microspores; f. Oval, pear-shaped, to elliptical microconidia. At lower center note two microspores as they arise from adjacent cells; g. Dichotomously branched microsporophore of *N. crassa,* microspores attached to parent cells, seen along the sides of the branches.

PLATE 24

a. *Neurospora tetrasperma.* The mycelium of race S_6 had grown out to the line on the second day after inoculation. Monilioid conidia from race S_1 were then placed on the spot marked *x*. Spermatization was not successful because these conidia had time to germinate. The new mycelium grew out rapidly and perithecia were formed in the usual way at the end of the fifth day. If the conidia had been placed on spot *y* back of the tip ends of hyphal growth, successful spermatization would have occurred and perithecia would have covered the spot, and not have been distributed widely as shown in this picture.

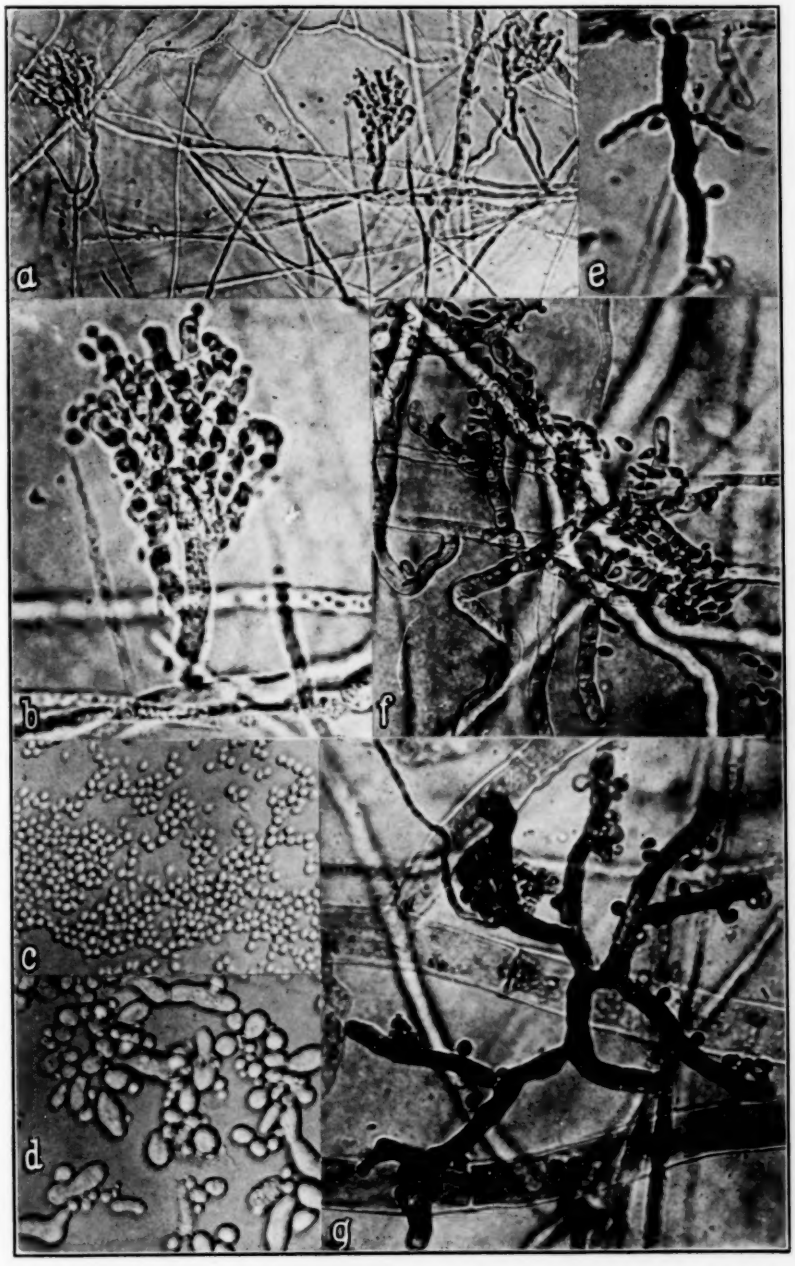
b. *N. sitophila,* race 56.6. Spermatization was effected with macroconidia on the two upper spots and with microconidia on the two lower spots. Perithecia appeared in all cases after 48 hours.

c. *N. sitophila,* race 56.6. Mycelium allowed to grow two days when it reached the line. Macroconidia from race 56.3 were then placed on the spot marked by the circle. Within the next 48 hours many perithecia developed as a result of successful spermatization with macroconidia.

d. Same as c except that microspores from race 56.2 were used for spermatization. Perithecia appeared on the spot after 48 hours.

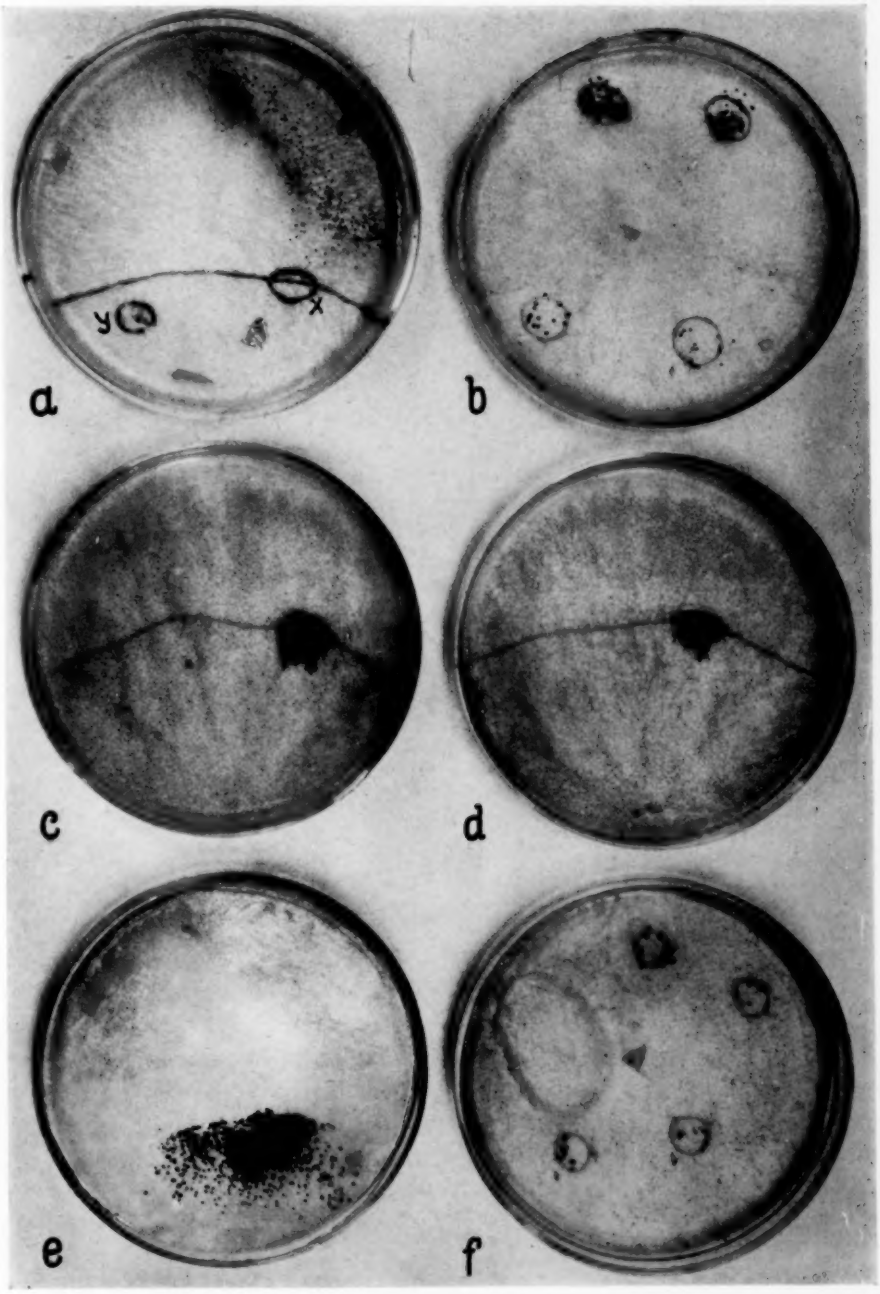
e. Plate culture inoculated on opposite sides with mycelia derived from second generation microspores obtained from races 56.2 and 56.6 respectively. Perithecia developed on the mycelium of the 56.6 race.

f. *N. tetrasperma.* After 3 days mycelium of S_1 was spermatized on the two upper spots with macroconidia from race S_6, and on the two lower spots with microspores from race S_6. Perithecia developed on all the spots after 4 days.



DODGE: NEUROSPORA

UNIV. OF MICH.



DODGE: NEUROSPORA

OF MICH

Studies on the flora of northern South America—XVII.

H. A. Gleason

A GROUP OF SPECIES IN MICONIA SECTION JUCUNDA

The section *Jucunda* of the great genus *Miconia* contained twelve known species in 1891, according to Cogniaux in his monograph of the family Melastomataceae. Since that time two others have been described, *M. involucrata* Donn. Sm. of Guatemala and *M. polita* Gl. of British Guiana, so that the section embraces to date fourteen species, while two additional species are described below. As a section, *Jucunda* is not well distinguished from *Tamonea*, its chief feature being the well developed triangular sepals, in contrast with the short sepals or scarcely developed calyx-lobes of *Tamonea*.

When representative material of this section is brought together, it is at once seen that eight of the species possess a number of common characters and form in themselves a compact species-group. So distinctive are these characters and so unlike those of other species of *Miconia* that the student of the genus is led to the conclusion that these plants represent a phylogenetic group of closely related species. The leaves are ample and pli-nerved. The flowers are sessile in small clusters subtended by conspicuous bracts (in *M. gratissima* the clusters are looser and the bracts probably smaller than in the others; I have never seen material in good flowering condition). The hypanthium is tubular and more slender than in most species of the genus. The ample calyx is deciduous at the torus at or soon after anthesis. The sepals are ovate or triangular and connivent or even connate in bud. In all except *M. holosericea* each sepal is prolonged into an unusually large and conspicuous exterior tooth, usually triangular in cross-section and completely concealing the sepal proper; in the excepted species the exterior tooth is merely a thickened protuberance. In five of the other seven species the free margin of the sepal proper is greatly reduced or lacking and may be easily overlooked, while in the last two, *M. acuminata* and *M. francavillana*, the true sepals are narrowly triangular or linear and about equal the exterior tooth in length. The pollen-sacs, together with a branch of the connective, are separated basally and prolonged below the insertion of the filament; the connective often bears a dorsal protuberance near its base. The ovary is a third to a half inferior, or even almost free. These floral characters are scarcely evident until the flower is dissected. On the herbarium sheet the exterior teeth invariably conceal the true sepals and may easily be mistaken for them.

The species may be separated by the following key:

Leaf-blades acute or cuneate at base, on petioles 1–3 cm. long.
Exterior tooth a minute thickening, about equaling the rounded tip of the sepal proper.....1. *M. holosericea.*
Exterior tooth slender, thin, about equaling the free triangular tip of the sepal proper 2. *M. acuminata.*
Exterior tooth thickened distally, truncate, about equaling the free subulate tip of the sepal proper.....3. *M. francavillana.*
Exterior tooth stout, triangular-pyramidal, much exceeding the sepal proper..... 4. *M. gratissima.*
Leaf-blades rounded, clasping, or connate at base, sessile or on petioles rarely more than 1 cm. long.
Flowers 6-merous; leaf-blades 7–13-pli-nerved; exterior tooth carinate on the inner side.
Bracts oblong, 5–8 mm. long.
Exterior tooth salient at nearly a right angle; anthers about 6 mm. long, dorsal protuberance none; ovary 4-celled.....5. *M. megaphylla.*
Exterior tooth erect; anthers about 4 mm. long, with a dorsal protuberance; ovary 3-celled.....6. *M. ampla.*
Bracts orbicular, 1 cm. long; exterior tooth erect.....7. *M. involucrata.*
Flowers 5-merous; leaf-blades 5-pli-nerved, clasping or connate at the sessile base; exterior tooth carinate on the outer side.....8. *M. fissa.*

1. MICONIA HOLOSERICEA (L.) Triana. For description and synonymy see Cogniaux, Monogr. Phaner. **7:** 732. Widely distributed from Rio de Janeiro (*fide* Cogniaux) through central Brazil (*Blanchet 603, 1808, Gardner*) to French Guiana (*Le Prieur, Jelski, Poiteau, Melinon, Broadway 728*), British Guiana (*Schomburgk 955/1303, 954/1264, Tate 252*), Trinidad (*Broadway 6455*), the Amazon Valley (*Spruce 1162*), Peru (*Williams 6435, Killip & Smith 24766, 24809*), and Bolivia (*Bang 1647, 1957, Rusby 2250*). It is typically an Amazonian species and the only common and widely distributed member of the group, as the citations above indicate, and the only one well represented in herbaria.

2. MICONIA ACUMINATA (Steud.) Naud. Cogn. *op. cit.* 731. French Guiana (*Martin*) and Surinam (*Hostmann 1265*).

3. MICONIA FRANCAVILLANA Cogn. Cogn. *op. cit.* 733. French Guiana (*fide* Cogn.); tropical Brazil (*Blanchet 3448*). Blanchet's specimen may be regarded as the type. Through the courtesy of the late Dr. Briquet I had opportunity to dissect a flower of the type, confirming beyond doubt the position of the species in this group. Cogniaux' plate indicates a deciduous calyx but fails to show the thickened exterior teeth.

4. MICONIA GRATISSIMA Benth. Cogn. *op. cit.* 732. French Guiana (*Melinon, Wachenheim 99*), British Guiana (*La Cruz 4526*), and the Amazon Valley (*Ule 5971, Spruce 1189*).

5. **Miconia megaphylla** sp. nov. Foliis amplis late ellipticis subsessilibus 9–13-pli-nerviis supra glabris subtus tenuissime tomentulosis; bracteis oblongis deciduis; floribus glomeratis sessilibus 6-meris; hypanthio tubuloso; calyce post anthesin deciduo; sepalis coriaceis ovatis, dentibus exterioribus magnis pyramidatis patulis; staminibus aequalibus, antheris subulatis arcuatis, connectivo simplice; ovario 4-loculare; stigmate truncato.

Stems stout, obscurely and roundly 4-angled, very thinly and closely tomentulose, appearing glabrous, marked by a conspicuous membrane 1–2 mm. wide at each node; petioles stout, pubescent like the stem, 2–3 mm. long; leaf-blades firm, broadly elliptic, as much as 30 cm. long by 19 cm. wide, rounded above to an apiculum 1 cm. long, obscurely crenate, broadly rounded at base, 9–13-pli-nerved, the uppermost laterals arising at about one-fourth the length of the leaf, only the upper two pairs continuous to the summit; upper surface glabrous, the veins conspicuous but nearly plane, the secondaries 6–10 mm. apart, spreading at an angle of 70–90°; lower surface very closely and minutely cinereous-tomentulose, the veins strongly elevated; panicle apparently about 13 cm. long, sparingly branched, its axes rather sharply 4-angled and pubescent with appressed stellate hairs, the nodes and flowers subtended by oblong deciduous bracts 6–8 mm. long; flowers in glomerules of 5–7, 6-merous, sessile; hypanthium tubular, thick-walled, 5.5 mm. long to the torus, thinly gray-tomentulose; calyx deciduous after anthesis, the sepals separate to the torus, thick and coriaceous, increasingly so above, rhombic-ovate, 3.3 mm. long, rather truncate above to a triangular apiculum; exterior teeth very stout and thick, pyramidal, 3-sided, 1.7 mm. long on top, salient at almost right angles, adnate to the sepals to their tips; petals narrowly obovate, 6.5–7 mm. long, rounded above, nearly equilateral, obscurely retuse or entire, glabrous; stamens isomorphic but variable in size; filaments slender, flat, about 6 mm. long; anthers subulate, somewhat arcuate, averaging about 6 mm. long, the pore dorso-terminal; connective simple, split near the base around the insertion of the filament, which therefore appears dorsal, and each half extending back over its theca to the base of the anther; ovary one-third inferior, thick-walled, 4-celled, its glabrous summit conic, obtusely 12-ribbed; style straight, stout, glabrous, 10 mm. long; stigma truncate.

Type, *Buchtien 1108*, collected at San Carlos, in the Mapiri region of Bolivia, alt. 750 m., and deposited in the herbarium of The New York Botanical Garden.

6. MICONIA AMPLA Triana. Cogn. *op. cit.* 729. Endemic to Trinidad (*Lockhart, Broadway 5855, 6144*).

7. MICONIA INVOLUCRATA Donn. Sm. Bot. Gaz. **37**: 209. 1904. Guatemala (*Tuerckheim 8204*) and British Honduras (*Schipp 377*).

8. **Miconia fissa** sp. nov. Caulibus validis glabris; foliis magnis sessilibus amplexicaulibus obovato-oblongis abrupte apiculatis 5-pli-nerviis utrinque glabris; paniculis congestis, floribus fasciculatis, bracteis magnis late rotunda-

tis, 5-meris; hypanthio cylindrico tomentuloso; calyce ad anthesin deciduo, sepalis triangularibus, dentibus exterioribus magnis pyramidatis; petalis obovato-oblongis glabris; antheris subulatis, connectivo ser. ext. supra basin elevato, ser. int. supra insertionem filamenti minute glanduloso; ovario 4-loculare semilibero, stylo elongato.

Apparently a tree or large shrub, with subterete glabrous branches greatly enlarged at the nodes; leaves membranous, oblong-obovate, as much as 22 cm. long by 12 cm. wide, at the tip obtuse or rounded, with an apiculum 10–15 mm. long, entire or obscurely crenate, sessile, certainly clasping, and apparently connate at base, glabrous and shining above, paler green and very minutely pubescent beneath, appearing glabrous, 5-pli-nerved, the uppermost primaries arising 20–25 mm. above the base, the secondaries plane and yellow above, rising at an angle of about 75°, 5–10 mm. apart, the tertiaries obscure above, with the secondaries elevated and reticulate beneath; panicles terminal and from the upper axils, in the former case branched from the base, crowded, 10–15 cm. long, of which the basal half is sterile, their axes rather sharply angled and gray-tomentulose, increasingly so distally; flowers sessile, 5-merous, in small dense clusters subtended by a pair of broadly rotund, tomentulose bracts 10–12 mm. long, composed of a central terminal flower and 2 sessile, lateral, 1–3-flowered clusters each subtended by a pair of similar bracts 8 mm. long and 6 mm. wide, the 1 or 2 lateral flowers of this cluster subtended by bracts 6 mm. long by 3 mm. wide; hypanthium cylindric, 7 mm. long to the torus, 3 mm. in diameter, ribless, closely gray-tomentulose or sericeous; calyx deciduous at or soon after anthesis, its tube prolonged about 0.8 mm.; sepals triangular, 5 mm. long over all, the sepals proper broadly ovate, 3 mm. long, the exterior teeth subterminal, stout, pyramidal, erect, surpassing the sepal proper by 2 mm.; petals obovate-oblong, 8 mm. long, 4 mm. wide, rounded above, glabrous, essentially equilateral, the basal half and a triangular central portion of the distal half fleshy in texture and veinless; stamens slightly dimorphic; filaments stout, flattened, glabrous, the exterior 6.5, the interior 4.8 mm. long; anthers stoutly subulate, nearly straight, 8–8.5 or 7.5 mm. long, opening by a terminal pore, 2-celled, the thecae strongly convoluted, prolonged about 1 mm. and somewhat divergent below the attachment of the filament; connective rounded on the back, near the base in the exterior series prominently elevated into a quadrate protuberance 1 mm. long, the interior series barely elevated into a low protuberance and bearing a conspicuous, sessile, hemispheric gland; ovary about half-inferior, 4-celled, its summit glabrous, narrowed to an erect beak; style 13 mm. long, very thinly and finely pubescent in the basal fourth, tapering to the apex; stigma hemispheric, barely expanded, 0.5 mm. in diameter.

Type, *Holt & Blake 528*, collected on the Rio Maturacá, below Salto de Huá, Amazonas, Brazil, 10–12 Dec. 1930, and deposited in the herbarium of The New York Botanical Garden. *Holt & Blake 468*, collected at the same place three weeks earlier, is the same but immature.

MICONIA SECTION ADENODESMA

Naudin erected the subgenus *Adenodesma* to include three species of *Miconia* with sessile leaves, large flowers, and glandular connectives. His concept was continued by Cogniaux forty years later as a section of the genus, without change in its definition and with the addition of two species which had been unknown to Naudin. Since then three other species have been described.

It is an open question whether a group of species with no more distinctive characters than those mentioned should be given the rank of subgenus or even of section. All three features occur repeatedly elsewhere in the genus, although this is the only group where they occur in conjunction. Careful dissection of the flowers of a majority of the species reveals that two distinct types of stamens are represented and that these types are correlated with equally distinct types of venation and leaf-form. In three species flowers have not been available, but the venation is sufficient to place them in one group or the other and it has been assumed that the stamens would follow the expected pattern if they were known.

The first of these groups contains only two species, *M. macrotis* Cogn. and *M. titanophylla* Gl. The former very closely resembles *M. Boissieriana* Cogn., now placed in the section *Tamonea*, and also suggests by its general habit and structure the common *M. macrophylla* (Don) Triana. These two species are accordingly transferred to *Tamonea*, but as a matter of convenience are still included in the key presented below. The second group includes nine species, all of which properly belong to the section *Adenodesma*. All have large flowers and glandular connectives, but the leaves are not invariably sessile, although always broad and large. In addition to these weak characters the group is distinguished sharply by the shape of the connective, as described more fully in the key below.

Leaves 7–13-nerved, the upper 5–7 primaries traversing the blade and the lower ones entering the conspicuous auricles; flowers often 6-merous. (Stigma, so far as known, capitate; connective, so far as known, prolonged straight back between the bases of the thecae and there obscurely lobed and minutely glandular.) Section TAMONEA, in part.

Leaves glabrous on the surface above, on the midvein thinly furfuraceous, plane; stem-pubescence of short, delicate, closely matted hairs, stellately branched at the tip, forming a dense indument about 1 mm. thick; flowers 6-merous. . . . *M. macrotis.*

Leaves bullate above, stellate-pubescent on the surface when young, soon becoming glabrate, permanently hirsute on the midvein; stem-pubescence of stout, densely matted hairs, sparsely plumosely branched and stellate toward the tip, forming an indument 4 mm. thick; flowers 5-merous. . . . . *M. titanophylla.*

Leaves 3–5-pli-nerved (sometimes weakly so), usually with an additional pair of obscure marginal veins, the primaries in most species preceded near the base of the

leaf by few to several secondaries; connective (so far as known) widened basally into two lateral deflexed lobes which extend ventrally over the sides of the thecae, are often confluent beneath and always conspicuously glandular, at least along their ventral margins. Section ADENODESMA.

Bracts inconspicuous, setaceous, early deciduous, rarely more than 3 mm. long; calyx open in bud, its lobes regular and obtuse or rounded, or none, the exterior teeth minute or none; stamens isomorphic or nearly so, the lateral lobes of the connective (so far as known) often confluent beneath; stigma not expanded; ovary 3–5-celled.

Stem-pubescence very close and fine, stellate-tomentulose or furfuraceous, forming an indument less than 1 mm. thick and often deciduous on the older parts; peduncle and branches of the inflorescence conspicuously angled.

Lower leaf-surface green, the actual surface plainly visible through the comparatively sparse indument of soft stellate hairs, these mostly limited to the veinlets and with a total spread of 0.2–0.7 mm.; anthers glandular at base of the connective only.

Leaves 3-pli-nerved, exclusive of the marginals; sepals triangular-ovate to semicircular; style and filaments more or less glandular; connective curved at base into a half-circle and bearing numerous glands on each lateral lobe; style 10–15 mm. long.

Leaves thin, obovate in general outline, usually broadest well above the middle, rather shortly acuminate, abruptly contracted below to a broad base which is rounded or cordate to the petiole.....1. *M. amplexans.*

Leaves firm, oblong-elliptic in general outline, broadest near the middle, rather long-acuminate, gradually acuminate below to a narrow base which tapers to the petiole.....2. *M. tomentosa.*

Leaves 5-pli-nerved, exclusive of the marginals; sepals broadly ovate; style and filaments glabrous; connective lightly curved at base and bearing two stalked glands on each lobe; style 5–6 mm. long.....3. *M. biglandulosa.*

Leaves weakly 5-pli-nerved; calyx-limb very thick, the sepals obsolete; style and filaments densely glandular; connective curved into a quarter-circle and densely glandular; style 21 mm. long.....4. *M. axinaeoides.*

Lower leaf-surface brown or rufescent, the actual surface completely concealed by the dense indument of sublepidote stellate hairs, covering the surface uniformly and with a total spread of 0.1–0.2 mm.

Leaf-blades dull above, long-acuminate, three times or more as long as broad, rounded or obtuse at base; connective glandular on the back; filaments and style densely glandular.....5. *M. Plukenetii.*

Leaf-blades shining above, acute to obtuse, twice or less as long as broad, distinctly cordate at base (stamens as yet unknown).....6. *M. silicicola.*

Stem-pubescence of stout, spreading, hirsute or plumose bristles 2–5 mm. long.

Leaves strongly bullate above; hypanthium both hirsute and stellate; sepals with a small exterior tooth; ovary 5-celled.....7. *M. rugosa.*

Leaves plane above; hypanthium merely stellate-tomentose; exterior teeth none; ovary 3-celled.....8. *M. plumosa.*

Bracts conspicuous, oblong or ovate, persistent to anthesis or later, 5–6 mm. long; calyx apparently closed in bud, the exterior teeth adnate, triangular, nearly 2 mm.

long; stamens strongly dimorphic, the lateral lobes of the connective in the smaller series not confluent beneath; style and filaments densely glandular; stigma capitate; ovary 5-celled.....9. *M. triangularis.*

1. MICONIA AMPLEXANS (Crueg.) Cogn. For description and synonymy see Cogniaux, Monogr. Phaner. **7:** 749; Gleason, Bull. Torrey Club **58:** 227. 1931; its geographical distribution is also discussed in the latter article.

2. MICONIA TOMENTOSA (L. C. Rich.) Don. Cogniaux, *op. cit.* 750. Common and widely distributed throughout the Amazonian region from Rio de Janeiro (*fide* Cogniaux) and Bolivia (*Williams 567*) to Trinidad; also in Cuba (*Roig & Van Hermann 1123*) and Isle of Pines (*Jennings 442*); most abundant in the Guianas. The variety *ovata* Cogn. (*Spruce 814*) is poorly distinguished by leaf-character only and should not be maintained. The variety *auriculata* Jennings (*Jennings 442*; type in herb. Carnegie Museum) is *M. macrophylla* (Don) Triana, as to type specimen and description; the sheet of the same number in the New York Botanical Garden is *M. tomentosa.* This species and *M. amplexans* are distinguished solely by the shape of the leaves and are connected by intergrading forms with the leaf-base wider than in typical *M. tomentosa* and narrower than in typical *M. amplexans.* The former is possibly the primitive form, occupying a rather compact area in northeastern South America, while the latter occurs chiefly at the margin of this area. I have maintained both species more for historical reasons than because of actual structural differences.

3. **Miconia biglandulosa** sp. nov. Arbuscula, ramis 4-sulcatis densissime stellato-furfuraceis; foliis firmulis sessilibus oblongo-obovatis acuminatis subintegris ad basin subcordatam cuneatis 5-pli-nerviis, supra ad venas furfuraceis ceterum glabris, subtus brunneis stellato-pubescentibus; panicula angustata dense furfuracea; floribus sessilibus 5-meris; hypanthio cylindrico tomentosulo; calycis lobis ovatis obtusis; petalis oblongo-obovatis; staminibus subisomorphis; filamentis glabris; antheris subulatis subrectis, connectivo ad basin curvato dorsaliter paullum elevato, lobis lateralibus ad marginem glandulis 2 ornatis.

A tree 3–5 m. high, the younger branches conspicuously but roundly 4-angled and 4-sulcate, densely and closely stellate-furfuraceous with bright brown hairs; leaves firm, sessile, oblong-obovate, 25–35 cm. long, 10–15 cm. wide, sharply acuminate, subentire, cuneately narrowed from below the middle to a subcordate base, 5-pli-nerved, with an additional pair of marginal veins in the basal half only, veins all plane above, elevated beneath, the secondaries 5–9 mm. apart, ascending at an angle of about 70, the upper side thinly furfuraceous on the primaries, otherwise glabrous, the lower side rather densely stellate-pubescent, especially on the veins; panicle narrow, 20 cm. long, densely brown-furfuraceous like the stem, freely branched, the bracts setaceous, 2 mm. long; flowers sessile, 5-merous; hypanthium cylindric,

5 mm. long to the torus, densely and softly stellate-tomentose; calyx-tube prolonged about 1 mm., the sepals broadly ovate, 0.8 mm. long, very obtuse, pubescent externally like the hypanthium; exterior teeth minute, subterminal; petals narrowly oblong-obovate, 5 mm. long, 2.2 mm. wide, inequilateral, retuse, essentially glabrous; stamens isomorphic but slightly different in size; filaments slender, glabrous, 4 or 5 mm. long; anthers subulate, slightly arcuate, 4 or 5 mm. long, 2-celled; connective slender, elevated near the base into a low dorsal protuberance, the sides of which extend ventrally into 2 lateral lobes over the thecae and bear at the margin of each 2 short-stalked glands; ovary nearly free, subcylindric, 2.8 mm. long, 3-celled, glabrous; style stout, glabrous, 5.6 mm. long, the truncate stigma 0.5 mm. in diameter.

Type, *Killip & Smith 26933*, collected in woods at Iquitos, Peru, alt. about 100 m., and deposited in the herbarium of The New York Botanical Garden. The field notes indicate that the petals are greenish white, the filaments and style white, and the anthers purple.

4. **Miconia axinaeoides** sp. nov. Ramis crassis dense brunneo-tomentosis; petiolis brevibus dense tomentosis; laminis amplis membranaceis late obovatis sursum rotundatis breviter apiculatis integris basi late obtusis sub-5-plinerviis, supra ad venam mediam inferne tomentellis ceterum glabris, subtus ad venas venulasque tenuiter tomentosis ceterum glabris; panicula subsessile pauciflora dense et tenuiter stellato-tomentosa; floribus 5-meris breviter pedicellatis; hypanthio turbinato tenuiter stellato-pulverulento; calycis tubo subampliato truncato, dentibus exterioribus minutis subulatis; petalis obovato-oblongis magnis; staminibus isomorphis; filamentis elongatis complanatis dense glanduloso-pubescentibus; antheris lineari-subulatis thecis convolutis; connectivo basi dilatato in lobos 2 laterales producto ad marginem ventralem stipitato-glandulosos; ovarium inferum 4 (forsan 5)-loculare; stylo elongato glanduloso-pubescente, stigmate parvo.

Upper stems stout and woody, probably considerably flattened,densely brown-tomentose; petioles very stout, 15 mm. long, densely tomentose like the stem; leaf-blades thin and membranous, broadly obovate-oblong, 20–31 cm. long, 13–18 cm. wide, broadly rounded above to a subapiculate tip, entire, broadly obtuse or subrotund at base, weakly 5-pli-nerved, glabrous above except for a little pubescence near the base of the midvein, glabrous beneath on the actual surface, thinly stellate-tomentulose on the veins; secondary veins 6–9 mm. apart, at right angles to the primaries, all veins nearly plane above, lightly elevated and prominently reticulate beneath; panicle nearly sessile, 10 cm. long, its slender axes closely but thinly stellate-tomentose, the lateral branches 2–3-flowered; flowers 5-merous, on pedicels 1–2 mm. long; hypanthium turbinate, 5 mm. long to the torus, very thick and hard, thinly stellate-furfuraceous when young; calyx somewhat spreading, prolonged 2.5 mm. and truncate, the sepals obsolete, the exterior teeth stoutly subulate, 0.6 mm. long, not projecting; petals obovate-oblong, 16 mm. long,

8 mm. wide, nearly equilateral, slightly retuse, glabrous; stamens isomorphic; filaments flat, 14 mm. long, densely glandular-pubescent throughout; anthers linear-subulate, 8.5 mm. long, slightly arcuate, 2-celled, the pollen-sacs strongly convolute; connective somewhat elevated and conspicuously widened at the base, prolonged into two lateral lobes covering the base of the pollen-sacs and stipitate-glandular along the ventral margin; ovary small, inferior, 4- or 5-celled; style somewhat sigmoid and declined, stout, 21 mm. long, densely glandular-pubescent throughout; stigma small, truncate.

Type, *Buchtien 1099*, collected at Sarampiuni, near San Carlos, in the Mapiri region of Bolivia, alt. 600 m., and deposited in the United States National Herbarium, no. 1399445 (duplicate in herb. New York Botanical Garden). Its large flowers and turbinate hypanthium give it an aspect remarkably like an *Axinaea*.

5. MICONIA PLUKENETII Naud. Cogn. *op. cit.* 751. From French Guiana (*Wachenheim*) to British Guiana (*Schomburgk 1008/1727b, Hohenkerk 784, Appun 653, Stockdale 8762, Abraham 105, La Cruz 3600*) and Trinidad (*Crueger, Lockhart, Broadway*).

6. MICONIA SILICICOLA Gl. Bull. Torrey Club **58:** 428. 1931. Mount Roraima (*Tate 212*) and Mount Duida (*Tate 71*).

7. MICONIA RUGOSA Triana. Cogn. *op. cit.* 751. Manáos, Brazil (*Spruce 1718*); apparently known only by the type specimen.

8. MICONIA PLUMOSA Gl. Bull. Torrey Club **52:** 381. 1925. British Guiana (*Gleason 901, Sandwith 272*).

9. **Miconia triangularis** sp. nov. Arbor parva, ramis 4-sulcatis tenuissime stellato-furfuraceis; foliis sessilibus obovatis breviter acuminatis basi rotundatis vel subcordatis 3-pli-nerviis, ad venas utrinque et ad venulas subtus furfuraceis ceterum glabris; panicula angustata, bracteis late oblongis vel obovatis, floribus sessilibus 5-meris; hypanthio campanulato dense stellato; calyce irregulariter fisso hypanthium aequante utrinque pubescente, dentibus exterioribus triangularibus; petalis obovatis inaequilateralibus; staminibus dimorphis connectivo basi glanduloso; ovario 5-loculare.

A tree 3–6 m. high, the younger branches roundly 4-angled and 4-sulcate, thinly but closely stellate-furfuraceous; leaves sessile, firm in texture, obovate to oblong-obovate, as much as 13 by 25 cm., abruptly short-acuminate, minutely and irregularly crenate-denticulate, narrowed from the middle or above it to a rounded or subcordate base, 3-pli-nerved, secondaries arising at an angle of about 80°, 4–8 mm. apart, essentially glabrous above, very thinly furfuraceous on the veins and secondaries beneath; panicle rather narrow, 20–30 cm. long, its branches conspicuously 4-angled and 4-sulcate, tomentulose like the stem; bracts obovate to broadly oblong, 5–6 mm. long, subtending each flower and node, eventually deciduous; flowers sessile, 5-merous; hypanthium campanulate, 3.2 mm. long to the torus, densely and

finely stellate-tomentulose; calyx apparently closed in bud, at anthesis its tube prolonged 2.5 mm., densely sericeous within, its lobes irregularly triangular, lacerate, 1.6 mm. long; exterior teeth totally adnate, thick and heavy, triangular, about 2 mm. long; petals elliptic, 9 mm. long, 5 mm. wide, conspicuously inequilateral, slightly retuse; filaments densely glandular-pubescent throughout, 8.5 or 6.5 mm. long; anthers 2-celled, subulate, 7.5 or 5.7 mm. long; lateral lobes of the connective in the outer series almost confluent beneath the anther, densely glandular on the lower half, in the inner series extending halfway over the side of the anther and bearing a single marginal row of glands; ovary partly inferior, 5-celled, its free summit very broadly truncate; style 15 mm. long, densely glandular-pubescent; stigma capitate, 1.5 mm. in diameter.

Type, *Klug 1697*, collected at Umbria on the Putomayo River, Colombia, lat. 0°54′ N., long. 76°10′ W., alt. 325 m., and deposited in the herbarium of The New York Botanical Garden; *Klug 1790*, from the same locality, is identical.

PIPTOCARPHA IN ANDEAN SOUTH AMERICA

Piptocarpha R. Br. is a genus of vernonioid composites, distinguished from *Vernonia* chiefly by the caudate anthers and in a majority of the species also by the dense axillary inflorescences. The genus is best developed in southern and eastern Brazil, whence about twenty-five species are known. A few others occur in the Guianas, Trinidad, and Central America. Nine species have been accredited to the Andean region, ranging from Colombia to Bolivia. Of these, *P. elaeagnoides* Baker is best restored to the genus *Vernonia* as *V. elaeagnoides* HBK., and *P. gracilis* Rusby is *Vernonia gracilis* HBK. To the remaining seven there are now to be added four additional, hitherto undescribed species.

Schultz Bipontinus monographed the genus in 1863, under the name *Carphobolus*, basing his six subgenera largely on the character of the inflorescence. Baker followed essentially the same divisions in his treatment of the genus for the Flora Brasiliensis in 1873, and the same characters are again used in the key below, by which eleven Andean species may be separated.

Inflorescences and individual heads both sessile, axillary; leaves ovate-lanceolate, rounded at base, loosely stellate-pubescent beneath; heads with 11 flowers or more.

Heads 11–15-flowered; involucre 10 mm. high..... *P. asterotrichia.*

Heads about 34-flowered; involucre 15 mm. high..... *P. insignis.*

Inflorescences sessile, axillary, the individual heads distinctly pedicelled, forming a sessile umbel; heads about 15-flowered; involucre about 8 mm. high.... *P. Lechleri.*

Inflorescences peduncled, axillary, the peduncles few, short, stout, and umbellate, bearing each a few sessile heads; leaves finely canescent-tomentulose beneath.

Heads about 6-flowered; leaves mostly broadly obtuse or rounded at base..... *P. Poeppigiana.*

Heads about 11-flowered.

Flowers 1–3 on each peduncle; leaves of a lanceolate type, broadest below the middle, rounded or obtuse at the usually inequilateral base....*P. vismiaefolia.*

Flowers 5–10 on each peduncle; leaves of an elliptic type, broadest at the middle and acute at both ends.....*P. longifolia.*

Inflorescence a branched, axillary, corymbiform cluster.

Heads 3-flowered.....*P. Sprucei.*

Heads 5–6-flowered.

Leaves loosely stellate-pubescent beneath; stems pubescent; branches of the inflorescence and involucral scales densely gray-tomentose.....*P. canescens.*

Leaves densely and closely canescent beneath with a sublepidote tomentum; branches of the inflorescence and involucral scales glabrous or nearly so; stems finely canescent.

Petioles 15–25 mm. long; inflorescences loosely branched, 2–4 cm. long.... *P. laxa.*

Petioles about 10 mm. long, about equaling the influorescences..... *P. tereticaulis.*

Inflorescence a loose, open, freely branched, many-headed, terminal panicle..... *P. Sodiroi.*

Piptocarpha insignis sp. nov. Ramis crassis angulatis primum stellato-pubescentibus mox glabrescentibus; petiolis brevibus crassis tomentosis; laminis ovato-ellipticis acutis basi rotundatis supra scabridulis subtus stellato-pubescentibus venis reticulatis; capitulis sessilibus in axillis inferioribus 5–8 in superioribus paucis vel solitariis, 34-floris; involucri magni obconici squamis adpressis ovato-lanceolatis pungentibus acuminatis; floribus cum paleis linearibus immixtis; achaeniis glabris; pappo albido uniseriato.

A shrub 1.5–2 m. high, the upper branches stout, strongly angled, densely but evanescently stellate-pubescent, the internodes 3–5 cm. long or much shorter at the summit of the stem; petioles stout, 8 mm. long, densely stellate-tomentose; leaf-blades ovate-elliptic to ovate-oblong, firm, opaque, about 15 cm. long by 6.5 cm. wide, acute, entire, rounded at the inequilateral base, the upper side thinly pubescent on the midvein, minutely scabrellate on the surface, the secondary veins slightly impressed, the veinlets obscure, the lower side stellate-pubescent with stalked hairs bearing 3 or 4 terminal branches, thinly so on the surface, densely on the midvein, the veins and veinlets elevated and conspicuously reticulate; inflorescences axillary, forming clusters of 5–8 sessile heads in the lower axils, reduced to few or solitary heads and approximate at the summit of the branch; heads about 34-flowered; involucre obconic when pressed, 15 mm. long, its scales appressed, ovate-lanceolate, pungently acuminate, glabrous; flowers subtended by linear acuminate scales 12 mm. long; achenes glabrous, angulate, 4 mm. long; pappus nearly white, 7 mm. long, an outer series not differentiated.

Type, *Killip & Smith 26083*, collected in dense forest at San Nicolas, Pichis Trail, Dept. Junín, Peru, alt. about 1100 m., and deposited in the herbarium of The New York Botanical Garden.

Piptocarpha vismiaefolia sp. nov. Ramis gracilibus subteretibus tenuiter canescentibus; petiolis elongatis canescentibus; laminis lanceolatis mediocris acuminatis basi obtusis, supra praeter venam mediam pubescentem glabris subnitentibus, subtus canescenti-tomentosulis venis elevatis reticulatis; pedunculis paucis crassis brevibus axillaribus, capitulis in quoque pedunculo 1–3 sessilibus terminalibus parvis 6-floris; floribus achaeniis et pappo ignotis.

A shrub 3–4 m. tall, the upper branches slender, slightly angled, thinly cinereous-tomentulose, the internodes 3–4 cm. long; petioles rather stout, 15–20 mm. long, densely cinereous-tomentulose; leaf-blades firm, lanceolate, as much as 16 cm. long by 5.5 cm. wide, long-acuminate, entire, rounded or obtuse at the usually inequilateral base, the upper side minutely pubescent on the midvein, glabrous and somewhat shining on the surface, the veins and veinlets nearly plane and very finely reticulate, the lower side densely cinereous-tomentulose with sublepidote hairs, the veins and veinlets prominently elevated and reticulate; inflorescence axillary; peduncles several (about 5), stout, 3–5 mm. long, densely brown-tomentulose, each bearing 1–3 sessile terminal 11-flowered heads; involucre subglobose when young, becoming campanulate in age, 4–5 mm. long, its scales broadly ovate, obtuse, thinly pubescent when young, glabrous at maturity; flowers, achenes, and pappus immature in the type.

Type, *Killip & Smith 23848*, collected in dense forest east of Quimirí Bridge, near La Merced, Dept. Junín, Peru, alt. 800–1300 m., bearing immature flowers in June, and deposited in the herbarium of The New York Botanical Garden; *Williams 6675*, from Alto Río Huallaga, Dept. San Martín, alt. 360–900 m., with mature empty involucres in December, is the same.

Piptocarpha longifolia sp. nov. Ramis gracilibus subangulatis tenuiter canescentibus; petiolis angulatis elongatis dense tomentosulis; foliis anguste ellipticis acuminatis basi acutis supra glabris venis planis, subtus canescenti-tomentosulis venis elevatis reticulatis; pedunculis paucis crassis brevibus axillaribus; capitulis 13-floris in quoque pedunculo 5–10 sessilibus vel breviter pedicellatis; involucri ovoidei squamis late ovatis obtusis parce ciliatis; floribus cum paleis immixtis.

A slender tree 3–4 m. tall, the upper branches apparently elongate, slender, conspicuously angled, very thinly cinereous-tomentulose, the internodes 3–5 cm. long; petioles slender, strongly angled, 15–20 mm. long, densely cinereous-tomentulose; leaf-blades firm, narrowly elliptic or elliptic-oblong, as much as 21 cm. long by 6 cm. wide, broadest at the middle, sharply but abruptly acuminate, entire, acute at the base, glabrous above with plane veins and finely and inconspicuously reticulate veinlets, densely gray-tomen-

tulose beneath, the veins and veinlets strongly elevated and prominently reticulate; inflorescences axillary, each flowering node bearing several (3–6), stout, somewhat flattened, densely tomentulose peduncles 5–10 mm. long; heads 5–10 on each peduncle, sessile or on pedicels as much as 2 mm. long, 13-flowered; immature involucres ovoid, 4–5 mm. long, the scales appressed, broadly ovate, obtuse, often minutely ciliate; flowers (now immature) mingled with subtending scales.

Type, *Killip & Smith 25459*, collected in dense forest at Yapas, Pichis Trail, Dept. Junín, Peru, alt. 1350–1600 m., and deposited in the herbarium of The New York Botanical Garden.

Piptocarpha canescens sp. nov. Foliis magnis ovato-lanceolatis basi rotundatis supra opacis reticulatis subtus dense stellato-pubescentibus venis elevatis et arcte reticulatis; cymis axillaribus globosis multifloris congestis ramosis pedunculo brevioribus, ramis tomentosis gracilibus; involucri ovoidei 6-flori squamis adpressis ovatis acutis ad apicem tomentosis.

A tree 3–4 m. high, the upper branches slender, apparently elongate, nearly terete, densely pubescent with grayish hairs, the internodes about 5 cm. long; petioles stout, 1–2 cm. long, densely tomentose; leaf-blades thin, ovate-oblong to elliptic-oblong, as much as 21 cm. long by 10 cm. wide, broadest at or below the middle, subacuminate, entire, broadly rounded at base, the upper side densely stellate-pubescent on the midvein, essentially glabrous on the opaque surface but probably thinly stellate-pubescent when young, the lower side rather softly pubescent with stalked stellate hairs bearing 3–5 spreading terminal branches; primary and secondary veins impressed above, elevated beneath, the veinlets elevated and finely reticulate on both sides; inflorescences axillary, about 2 cm. in diameter when pressed, freely branched, each with about 40 heads, the branches slender, densely stellate-tomentose; pedicels about 1 mm. long; immature involucres campanulate or ovoid, 3–4 mm. high, the scales ovate, acute, densely tomentose on the exposed tips; flowers 6, the corollas, achenes, and pappus immature in the type.

Type, *Killip & Smith 26084*, collected in dense forest at San Nicolas, Pichis Trail, Dept. Junín, Peru, alt. about 1100 m., and deposited in the herbarium of The New York Botanical Garden.

The recent collections by Killip & Smith also include the following species:

Piptocarpha asterotrichia (P. & E.) Baker. San Ramón, Dept. Junín. 900–1300 m., *24747*.

Piptocarpha opaca (Benth.) Baker. Manáos, Brazil, *30111*.

Piptocarpha Poeppigiana (DC.) Baker. Lower Río Huallaga below Yurimaguas, Dept. Loreto, *28803*; Iquitos, Dept. Loreto, *26913*; along Río Marañon, near mouth of Río Tigre, *27527*, *27529*. The last specimen cited has conspicuously broader leaves, truncately rounded at the base.

TWO PERUVIAN SPECIES OF VERNONIA

Vernonia Fieldiana sp. nov. *Scorpioideae Foliatae*, caule subterete tenuiter tomentoso; foliis firmulis subsessilibus ovato-oblongis subacuminatis integris basi rotundatis, utrinque dense sed inconspicue pubescentibus, venis lateralibus curvato-adscendentibus subtus prominentibus; inflorescentia congesta multiflora, bracteis minutis; capitulis sessilibus 11-floris; involucri squamis laxe imbricatis acutis non carinatis subtomentosis ex infimis triangularibus ad interiores ovato-lanceolatas variantibus; corollae tubo lobos subaequante; achaeniis dense sericeis; pappi paleis lanceolato-oblongis quam setis interioribus albis 4–5-plo brevioribus.

Upper stems slender, nearly terete, densely and closely cinereous-tomentose, the internodes about 1 cm. long; petioles stout, 1 mm. long; leaf-blades firm, dull green, ovate-oblong, as much as 35 mm. long by 19 mm. wide, sharply acute or subacuminate, entire, rounded at base, both sides closely but inconspicuously pubescent with minute slender hairs, lateral veins curved-ascending and parallel, strongly elevated beneath; inflorescence a crowded, many-flowered, compound, scorpioid cyme, its short axes densely and softly cinereous-tomentose; bracts seldom more than 5 mm. long; involucre campanulate when dry, 5 mm. high, its scales loosely imbricate, sharply acute, not carinate, densely subtomentose, the outermost triangular, the inner ovate-lanceolate and as much as 3.4 mm. long; flowers 11 in each head; corolla 5 mm. long, the tube about equaling the lobes, glabrous; anthers 2.2 mm. long; style-branches 1.5 mm. long; achenes densely sericeous; paleae lanceolate-oblong, 0.8 mm. long; bristles white, 3.5 mm. long.

Type, *Williams 7663*, collected at San Roque, Dept. San Martín, Peru, alt. 1350–1500 m., and deposited in the National Herbarium as no. 1495545. *V. Fieldiana* closely resembles *V. Mandonii* Sch.-Bip. in foliage and general habit, but in the latter species the leaves are much more densely pubescent, the bracts are larger, the pappus is tawny, and the outer scales of the involucre are linear-subulate and subspinose at tip.

Vernonia albifila sp. nov. *Lepidaploa*, fruticosa erecta caule obscure angulato pubescente; foliis elliptico-oblongis acuminatis ad basin in petiolum brevem cuneatis minute denticulatis supra tenuiter papilloso-pubescentibus subtus minutissime albo-pubescentibus; panicula ampla ramosa pubescente; capitulis sessilibus sub-18-floris; involucri squamis adpressis brevibus subacutis arachnoideo-pubescentibus; corolla glabra; achaeniis obscure angulatis pubescentibus; pappi paleis linearibus, setis ca. 35 albidis.

Erect shrub 3 m. high, the upper branches slender, obscurely but rather sharply angled, thinly but closely pubescent, the internodes 2–3 cm. long; leaf-blades thin, elliptic-oblong, 7–9 cm. long, 2–3 cm. wide, sharply acuminate, cuneate at base into a petiole 3 mm. long, very minutely and remotely denticulate, lustrous and minutely papillose-pubescent above, minutely

pubescent with white hairs beneath; inflorescence a corymbiform panicle, freely branched, 15 cm. long and wide, leafless except at base of the lower branches, its axes softly pubescent; heads very numerous, sessile, about 18-flowered; involucre subglobose, campanulate when pressed, about 5 mm. high, its scales spirally imbricate, appressed, bluntly acute, arachnoid-pubescent, thin at the margins, dark-colored on the exposed tips, never carinate, ranging from ovate-triangular and 1.3 mm. long through ovate, 1.6 mm. long, to elliptic-oblong, 3.2 mm. long, and linear-oblong, 3.7 mm. long; corolla-tube 4.4 mm. long, gradually expanded distally, the lobes oblong-lanceolate, acute, 2.2 mm. long; anthers 2.8 mm. long, with lanceolate appendages 0.7 mm. long; styles minutely pubescent externally, their lobes 3.4 mm. long; achenes obscurely angled, 1.6 mm. long, thinly pilose; pappus-paleae linear-lanceolate, 0.4–0.6 mm. long; bristles about 35, nearly white, 5.6 mm. long.

Type, *Killip & Smith 30102*, from sandy woods at Manáos, State of Amazonas, Brazil, alt. 25 m., deposited in the herbarium of The New York Botanical Garden. The species is related to *V. polyanthes* (Spreng.) Less., which has longer and narrower, more densely pubescent leaves, thinner, blunter, and smoother involucral scales, and tawny pappus.

A NEW BLAKEA FROM COLOMBIA

Blakea bracteata sp. nov. Frutex scandens, ramis, petiolis, laminis, pedunculis et bracteis utrinque hirsutis; foliorum laminae oblongo-ellipticae breviter et anguste acuminatae, basi acutae 3-nerviae; pedunculi graciles axillares solitarii; bracteae externae late deltoideo-ovatae breviter acuminatae basi truncatae, internae oblongae acutae; hypanthium hemisphaericum glabrum; calyci limbus patens glaber, lobi triangulari-oblongi acuti hirsuti; petala obovata acuminata; filamenta antheras subaequantia; antherae in annulo conniventes crassae semi-ovoideae, poris 2 minutis terminalibus dehiscentes, connectivo crasso infra insertione filamenti brevissime producto et truncato.

A climbing shrub, the slender branches, petioles, leaf-blades, peduncles, and bracts hirsute throughout with purple-brown hairs 2–4 mm. long; leaves apparently equal and unequal in alternate pairs, the slender petioles 10–25 mm. long; blades thin, elliptic-oblong, as much as 13 cm. long by 5.5 cm. wide, abruptly short-acuminate, entire, acute or rarely obtuse at base, 3-nerved; veins not prominent, barely elevated beneath, the secondaries 3–5 mm. apart, ascending at an angle of 70°; peduncles solitary in the upper axils, 1–3 cm. long, slender; bracts separate to the base, the outer deltoid-ovate, 15 mm. long, 16 mm. wide, abruptly short-acuminate, broadly truncate at base, the inner oblong, 12 mm. long, 5 mm. wide, subacute, the basal third or half glabrous, the distal portion hirsute; flowers 6-merous; hypanthium hemispheric, glabrous, about 9 mm. in diameter; calyx membranous or nearly scarious, its glabrous tube spreading, 1.4 mm. wide, with broadly rounded sinuses; sepals triangular-oblong, thin, 4.5 mm. long, acute or subacute, densely hirsute on

both sides and margins; petals obovate, 13 mm. long, 8.5 mm. wide, acuminate glabrous except for 1 or 2 short bristles at the apex; filaments stout, flat, glabrous, 4 mm. long; anthers coherent in a ring, stoutly semi-ovoid, 4 mm. long, each theca opening separately by a minute terminal pore; connective very thick, barely prolonged below the filament into a fleshy truncate dorsal appendage; ovary wholly inferior, its top concave from sides to middle, where it is elevated into a short subcylindric beak; style straight, glabrous 8 mm. long; stigma subcapitate.

Type, *Klug 1669*, collected at Umbria, Comisaría del Putumayo, Colombia, at. 0° 54′ N., long. 76° 10′ W., alt. 325 m., in forest, and deposited in the herbarium of The New York Botanical Garden; *Klug 1824*, from the same locality, is identical.

The distant secondary veins give *B. bracteata* an aspect quite unlike other species of the genus. Hirsute pubescence and thin leaves are also the exception in *Blakea*. Our plant is apparent most nearly related to *B. hirsuta* Berg, in which the leaves are much larger and nearly smooth, the flowers subsessile, and the calyx glabrous.

THE NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE
1930–1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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